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Fishery Bulletin

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Vol. 77, No. 4

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Seattle, Washington

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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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REVISION OF THE PENAEID SHRIMP GENUS *PENAEOPSIS* (CRUSTACEA: DECAPODA)

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The genus *Penaeopsis*, comprising six species, is defined and its relationships discussed. Five of the species occur in the Indo-West Pacific, *P. balssi*, *P. eduardoi*, *P. challengeri*, *P. jerryi*, and *P. rectacuta*, and one, *P. serrata*, on both sides of the Atlantic. A key for their identification is provided. References, disposition of types, locality records, diagnoses, descriptions, and illustrations for each species are presented. The descriptions, except that of *P. balssi*, are based on material that includes type-specimens. The male of *P. challengeri*, which was not previously known, is described in detail. Intraspecific variation is noted, and distinguishing morphological features as well as affinities are discussed. In addition, geographic and bathymetric ranges are presented, and a graph of depth-temperature relationships of *P. serrata* in four areas within its range is included.

A study of the types of the three species of *Penaeopsis* described by Bate (1881) made obvious not only the need for redescriptions of these specimens, as was pointed out first by Burkenroad (1934a) and most recently by Ivanov and Hassan (1976), but also confirmed the necessity for a revision of the genus. As stated by Pérez Farfante (1977b), misidentifications, incomplete descriptions, and lack of detail in some of the illustrations presented by Bate (1881, 1888) have been responsible for much of the persistent confusion in the recognition of the species of *Penaeopsis*. The examination of Bate's types and the study of collections made during the cruises of 26 research vessels have enabled me to: clarify the problems associated with his work; describe two previously unnamed species (Pérez Farfante 1977b, 1979), as well as the male of another that had not been known before; prepare detailed accounts of the remaining members of the genus; and determine intraspecific variation. I have also discussed their affinities and delimited their respective geographic and bathymetric distribution. The distributional studies resulted in the restriction of the range of *P. rectacuta* and the considerable extension of that of *P. serrata*, the latter reported by Pérez Farfante and Ivanov (1979).

The species of the genus are benthic and, except in the eastern Pacific where none has been recorded, occur in the upper part of the continental and insular slopes of tropical, subtropical, and certain temperate regions of the world. All species have been found in the Indo-West Pacific, except *P. serrata*, which is restricted to the Atlantic, where it is present on both the eastern and western slopes. These shrimps are frequent and often abundant components of the catches made between 250 and 600 m, and two of the species are commercially exploited.

PRESENTATION OF DATA

In the account of the species, most of the terminology used for features of the petasma, thelycum, and appendix masculina follows that proposed by Pérez Farfante (1969, 1971). The measurement of rostrum length is the linear distance from apex to orbital margin, that of carapace length (cl) is the distance between orbital margin and the midposterior margin of the carapace, and, finally, that of total length (tl) is the distance from the apex of the rostrum to posterior end of the telson. All measurements are made to the nearest 0.5 mm. The petasmata have been described and depicted unfolded, and the illustrations made from stained specimens.

MATERIAL

Abbreviations of the repositories of the specimens examined during this study follow:

BMNH British Museum (Natural History), London.

[1]Systematics Laboratory, National Marine Fisheries Service, NOAA, National Museum of Natural History, Washington, DC 20560

Manuscript accepted June 1979.
FISHERY BULLETIN: VOL. 77, NO. 4, 1980.

FIU	Department of Biological Sciences, Florida International University, Miami, Fla.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
MP	Muséum National d'Histoire Naturelle, Paris.
ORI	Oceanographic Research Institute, Durban.
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden.
SAM	South African Museum, Cape Town.
UMML	Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Fla.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
VNIRO	All Union Research Institute of Marine Fisheries and Oceanography, Moscow.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Conn.
ZSI	Zoological Survey of India, Calcutta.

Penaeopsis Bate 1881

Penaeus. Bate 1881:173 [part]. Alcock and Anderson 1899:278. [Not *Penaeus* Fabricius 1798].

Penaeopsis Bate 1881:182 [type-species, *Penaeopsis serratus* Bate 1881, designated by Bouvier 1905a:981]; 1888:273. Bouvier 1905b:747; 1908:3. A. Milne Edwards and Bouvier 1909:220 [part]. De Man 1911:53 [part]. Balss 1925:228. Schmitt 1926:319 [part]. Burkenroad 1934a:48 [part, subgenus *Penaeopsis*]. Kubo 1949:320. Balss 1957:1519 [part]. Burkenroad 1959:285 [Neither *Peneopsis* Faxon 1895, or *Penaeopsis* Yokoya 1941, Barnard 1950]. Gender: feminine. Placed on the Official List of Generic Names in Zoology as Name 1821, International Commission on Zoological Nomenclature 1969, Opinion 864:139.

Parapenaeus Smith 1885:172 [part]. Alcock 1905:519 [part]; 1906:30 [part]. De Man 1911:77 [part]. Balss 1925:228.

Metapenaeus Wood-Mason 1891:271 [part].

Diagnosis.—Body slender, integument glabrous. Rostrum armed only with dorsal teeth; epigastric tooth separated from first rostral tooth by approximately 0.35 length of carapace; two low and sharp adrostral carinae, dorsal one running along bases of teeth. Carapace without longitudinal or transverse sutures; orbital and branchiostegal spines lacking; antennal and hepatic spines moderately long; pterygostomian spine well developed; cervical sulcus well defined, its posterior extremity placed slightly anterior to midlength of carapace, and relatively far ventral to dorsal midline; hepatic sulcus, reaching pterygostomian spine, well marked anteriorly, shallow posterior to hepatic spine; anterior part accompanied by sharp carina; branchiocardiac carina present. Abdomen carinate dorsally from fourth through sixth somites (carina rounded on fourth, keellike on posterior somites, continuous posterolaterally with paired short spines on fourth and fifth somites, and with sharp spine posteriorly); sixth somite bearing interrupted cicatrix on lateral surface, and pair of minute spines posteroventrally. Telson with median sulcus flanked by sharp carinae, and pair of moderately long, fixed lateral spines preceded by two or three pairs of small, movable spines. First article of antennular peduncle bearing long subdistal "parapenaeid spine" on ventromedian margin; antennular flagella with length about 0.75 to almost twice that of carapace; ventral flagellum sexually dimorphic, in male shorter than dorsal and strongly modified, with proximal part forming rigid, flattened, semicircular loop, bearing basal scale and ending distally in usually conspicuous, blunt knob; distal part straight and somewhat compressed. In female, ventral flagellum also bearing basal scale, but straight and longer than dorsal. Mandibular palp two jointed, proximal article short, subtriangular (oriented with base distally), distal article considerably longer than proximal, broadly oval. First maxilla with broad unjointed palp not produced distally. Flagellum of first maxilliped slender, overreaching distal exite of coxa. Third maxilliped lacking basial spine. Basial and ischial spines on first pereopod, always lacking on third. Exopods (small but not vestigial) on all maxillipeds and pereopods. Petasma symmetrical, lacking channeled, hornlike distolateral projections; dorsomedian lobule bearing distal and proximal plates; rib of dorsolateral lobule produced into conspicuous, flattened, proximal process. Appendix masculina small but well developed and relatively heavily sclerotized. Thelycum with well-developed median plate on

sternite XIII, plate on sternite XIV elongate and bearing paired seminal receptacles disposed longitudinally rather than transversely. Pleurobranchia on somites IX-XIII; rudimentary, filamentose arthrobranchia on somite VII, anterior and posterior arthrobranchiae on somites VIII-XII, and only posterior arthrobranchia on somite XIII. Epipod on first maxilliped (if proximal exite of coxa is considered an epipod) and second maxilliped and on first to third pereopods.

In this genus the petasma is structurally very simple, consisting of a plain trough that is neither produced as distal or distolateral hornlike or broad projections, nor bears distal elements associated with the four lobules. The pestasmal lobules are reinforced by plates and ribs: a distal plate and a proximal plate on the dorsomedian lobule, and two longitudinal ribs. One of the longitudinal ribs extends along the dorsolateral lobule and is typically produced proximally as a process the shape of which varies with the species, the other rib forms the ventral costa and occupies the free margin of the ventrolateral lobule. This petasma is similar to that of the genus *Penaeus*, but, in other respects, *Penaeopsis* does not resemble the latter; instead, it is closely related to *Metapenaeopsis* which, surprisingly, exhibits an asymmetrical petasma that is also the most complex among the Penaeoidea.

Small juvenile *Penaeopsis* are armed with an anteriorly directed, sharp spine on sternites XIII and XIV. Both spines disappear in larger males, whereas in females that on sternite XIII is either lost or persists, although considerably reduced, at the apex of the median plate, which, in itself, represents an expansion of the basal portion of the spine. The spine on sternite XIV disappears entirely or becomes incorporated in the median ridge or protuberance of that sternite. As Burkenroad (1934a) has stated, the occurrence of these sternal spines is a larval character present on the postmysis stages of many Penaeidae.

Despite the homogeneity of the few species (six, of which only four were known prior to 1976) currently assigned to the genus *Penaeopsis*, the first three described were assigned to two genera (Bate 1881). Subsequently, various authors have referred Bate's species to four different genera. Schmitt (1926) contributed to our knowledge of the genus when he recognized common superspecific characters in the "small '*Penaeopsis serratus*' group." Unfortunately, the characters he chose led him to include within this assemblage two species that are currently recognized as members of the genus *Metapenaeopsis*: *M. coniger* (Wood-Mason 1891) and *M. andamanensis* (Wood-Mason 1891). Schmitt cited the absence of anterior arthrobranchia on somite XIII as one of the characters of the "group," a valid *Penaeopsis* character common to all of the species except those two mentioned above, which he assigned to *Penaeopsis* although he was aware that they possessed such arthrobranchia.

A few years later Burkenroad (1934a) presented an enlightened discussion of two of the four Series—Parapenaeus and Trachypenaeus—into which he (1934b) divided the Penaeinae [= Penaeidae]. His excellent choice of characters for the definition of the genera resulted in very few changes in his classification during the 45 yr that have elapsed since the publication of the two contributions. Among the few alterations that have been made in the taxa recognized by him was the reelevation of *Metapenaeopsis* to generic rank; he had considered *Penaeopsis* and *Metapenaeopsis* to be subgenera of the genus *Penaeopsis*. The members of these two species-groups are closely allied, because both species-groups possess a carapace lacking longitudinal and transverse sutures but bearing pterygostomian spines, two or more well-developed movable spines on the lateral margins of the telson anterior to the fixed pair, and exopods on all maxillipeds and pereopods. However, the two taxa exhibit characters that are now considered to be of generic value, i.e., branchial formula, thelycal features, and basic structure of both the petasma and appendix masculina (for a detailed account of *Metapenaeopsis* see Pérez Farfante 1971). These characters were employed by Kubo (1949) in diagnosing the two groups as distinct genera, a revision that is now generally accepted.

Key to Species of *Penaeopsis*

1. Telson bearing three pairs of movable spines 2
   Telson bearing two pairs of movable spines 3

2. Hepatic spine situated at level of antennal spine; branchiocardiac carina long, its anterior extremity close to hepatic sulcus. Thelycum with plate of sternite XIV rounded anterolaterally; median plate of sternite XIII subsemicircular or weakly trilobed ..... *P. jerryi*
   Hepatic spine situated distinctly ventral to level of antennal spine; branchiocardiac carina short, its anterior extremity relatively far from hepatic sulcus. Thelycum with plate of sternite XIV angular anterolaterally; median plate of sternite XIII cordiform ..... *P. rectacuta*

3. Rostrum usually strongly arched, short, in adult reaching at most about midlength of second antennular article. Petasma with proximal process of rib of dorsolateral lobule transversely oval; ventral costa ending distally in broad, roughly semicircular process. Thelycal plate of sternite XIV produced in small lobules and with anterior border straight or, usually, concave on each side of posteromedian projection of sternite XIII; median ridge (sometimes reduced to posterior protuberance) flanked by broad depressions ..... *P. balssi*
   Rostrum not strongly arched, long, in adult overreaching (often considerably) second antennular article. Petasma with proximal process of rib of dorsolateral lobule subrectangular or nearly circular; ventral costa ending distally in spine or subelliptical process. Thelycal plate of sternite XIV weakly to strongly convex on each side of posteromedian projection of sternite XIII, and with neither median ridge nor posterior protuberance flanked by broad depressions 4

4. Petasma with ventral costa produced distally into long spine considerably overreaching level of row of cincinnuli. Thelycum with lateral borders of plate of sternite XIV turning abruptly mesially posterior to midlength, plate bearing short, pedunculate posteromedian protuberance ..... *P. eduardoi*
   Petasma with ventral costa ending distally in blunt, short process or spine not overreaching level of row of cincinnuli. Thelycum with lateral borders of plate of sternite XIV not turning abruptly mesially posterior to midlength, plate bearing long, median ridge or short, subrectangular posteromedian protuberance 5

5. Petasma with ventral costa bearing distolaterally short, flexible projection, and ending distally in rather slender spine, not overreaching level of row of cincinnuli. Thelycum with plate of sternite XIV raised in paired submesial elevations, not produced in lobules anterolaterally, and bearing short, subrectangular posteromedian protuberance sometimes continuous with depressed ridge ..... *P. challengeri*
   Petasma with ventral costa lacking projection, and ending distally in blunt, relatively broad process. Thelycum with plate of sternite XIV raised laterally, produced in lobules anterolaterally and bearing long, ovoid, tear-shaped or subtriangular ridge ..... *P. serrata*

Penaeopsis balssi Ivanov and Hassan 1976

Figures 1-6

Penaeopsis challengeri?. Balss 925:228, fig. 4 [not *Penaeopsis challengeri* De Man 1911].

Penaeopsis serratus. Ramadan 1938:68, fig. 13a-d [not *Penaeus serratus* Bate 1881, or *Penaeopsis serratus* Bate 1881].

?*Penaeopsis rectacuta*. Kensley 1969:154 [not *Penaeus rectacutus* Bate 1881].

Penaeopsis rectacuta. Kensley 1972:20, fig. 8G-I [not *Penaeus rectacutus* Bate 1881].

Penaeopsis serrata. Starobogatov 1972:390, fig. 40. Crosnier and Jouannic 1973:11, pl. 2, fig. 3 [not *Penaeus serratus* Bate 1881, or *Penaeopsis serratus* Bate 1881].

Penaeopsis balssi Ivanov and Hassan 1976:1, fig. 1-2 [holotype, ♀, Zool. Mus. Acad. Sci. U.S.S.R. Leningrad, 1/62552; type-locality, off southern Mozambique, 25°26′ S (not 23°26′ S as stated in original description, Boris G. Ivanov[2]), 33°31′ E, 410 m, *Van Gogh* stn 264]. Pérez Farfante 1977b:173.

Material.

KENYA—2♀, BMNH, off mouth of Tana

[2]Boris G. Ivanov, All Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow, pers. commun. 1979.

River, Kipini, staff Institute of Oceanographic Sciences. 3♀, BMNH, off Formosa Bay, 290 m, 15 February 1975, staff Institute of Oceanographic Sciences. 1♂ 1♀, USNM, off Ras Ngomeni, 300-310 m, 12 December 1975, *Professor Mesyatsev*. 4♀, BMNH, off Kenya, 15 February 1975, staff Institute of Oceanographic Sciences.

TANZANIA—3♀, BMNH, Pemba Channel, 329 m [in Sewell 1935], 14 January 1934, John Murray Expedition stn 110. 1♀, BMNH, Pemba Channel, 439 m, 12 January 1934, John Murray Expedition stn 107. 11♂ 17♀, BMNH NW of Zanzibar I, 280 m, 11 January 1934, John Murray Expedition stn 105A. 2♂ 2♀, RMNH, off Kunduchi, 20 km N of Dar es Salaam, 370-400 m, July 1974, C. Sankarankutty.

MOZAMBIQUE—4♀, USNM, Monte Belo, 270 m, 28 October 1975, E. Sorensen.

SOUTH AFRICA—4♂, USNM, 1♀, ORI, off Zululand, Natal, 280 m, A. J. de Freitas. 3♂ 11♀, SAM-USNM, off Natal, 454-280 m, 25 May 1975, *Meiring Naude* stn SM15.

Diagnosis.—Rostrum arched (usually strongly so) and short, reaching at most midlength of second antennular article. Anteroventral angle of carapace obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing strong mesial crest; proximal process of rib of dorsolateral lobule suboval and directed mesially; ventral costa ending distally in roughly semicircular process. Thelycal plate of sternite XIV with anterior border usually concave on each side of posteromedian projection of sternite XIII and distinctly slanting posterolaterally; median ridge broadest and highest posteriorly, usually gently tapering anteriorly (sometimes reduced to posterior protuberance), and flanked by deep, broad depressions; median plate of sternite XIII subtriangular to orbicular.

Description.—Rostrum (Figure 1) usually markedly arcuate (always strongly so in young), deep basally, and short, in adult reaching at most midlength of second antennular article, its length ranging from about 0.35 to 0.45 that of carapace. Rostral plus epigastric teeth 9-13; rostral teeth evenly spaced and close together along entire margin, second rostral tooth, occasionally third, located in line with orbital margin. Postrostral carina extending posteriorly for short distance beyond epigastric tooth, ending at level of dorsal extremity of cervical sulcus; small dorsal tubercle (occasionally indistinct) located near posterior margin of carapace. Antennal spine slender, sharp, and followed by short but well-defined carina; hepatic spine about as long as, and positioned ventral to but close to level of, antennal spine. Anteroventral angle of carapace (ventral membrane excluded) moderately to broadly obtuse (Figure 2*A*). Cervical carina sharp, accompanying sulcus well marked; hepatic carina descending obliquely in arc anteroventrally from below hepatic spine, then continuing in almost straight line to apex of pterygostomian spine; hepatic sulcus barely distinct posteriorly; branchiocardiac carina strong to almost indistinct, extending posterodorsally in arc, occasionally in sigmoidal curve, from behind hepatic sulcus to rather near posterior margin of carapace.

Mandible, first maxilla, and first maxilliped as illustrated (Figure 3 *A-C*).

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.65 as long as second in former and 1.45 in latter; prosartema falling conspicuously short of distal margin of eye, but its long setae reaching that far; stylocerite ending in small spine, length about 0.4 that of first article; distolateral spine long, slender, and sharp, reaching base of distal

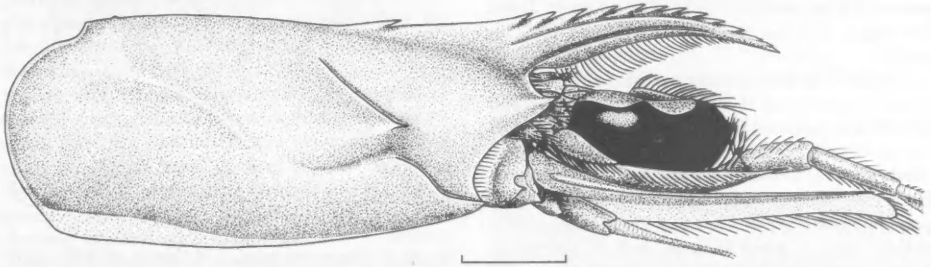

FIGURE 1.—*Penaeopsis balssi*, ♀ 21.5 mm cl, Formosa Bay, Kenya. Cephalothorax, lateral view. Scale = 5 mm.

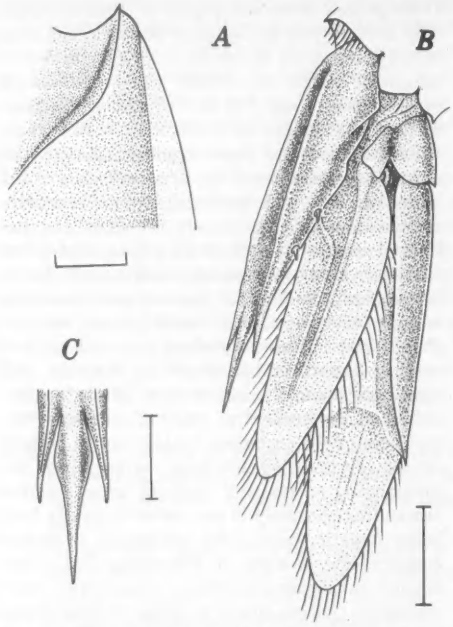

FIGURE 2.—*Penaeopsis balssi*, ♀ 21.5 mm cl. Formosa Bay, Kenya. *A*, Anteroventral part of carapace. *B*, ♂ 25 mm cl, off Kunduchi, 20 km N of Dar es Salaam, Tanzania. Telson and right uropod, lateral view. *C*, Same specimen, tip of telson, dorsal view. Scales: *A*, *C* = 2 mm; *B* = 5 mm.

0.3 of second article. Flagella in both male and female similar to those of *P. rectacuta* (see p. 743).

Scaphocerite falling short of, or slightly overreaching, distal end of antennular peduncle; lateral rib ending in sharp spine not quite reaching terminal margin of lamella. Antennal flagellum incomplete in specimens studied.

Third maxilliped extending at least to base of second antennular article and at most to distal 0.4 length of third; ratio of dactyl/propodus 0.75-0.80.

First pereopod extending to distal end of carpocerite or exceeding it by length of dactyl. Second pereopod surpassing carpocerite at least by dactyl and at most by propodus and 0.2 length of carpus (also reaching between distal 0.3 of first antennular article and about midlength of second). Third pereopod reaching at least to midlength of second article and at most to near end of peduncle. Fourth pereopod overreaching carpocerite by 0.8 length of dactyl or by as much as length of dactyl and propodus. Fifth pereopod extending to distal 0.2 of first article or as far as distal 0.3 of second. Order of pereopods in terms of their maximum anterior extensions: first (shortest), fourth, second, fifth, and third. Third maxilliped falling slightly short of third pereopod.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing almost indistinct, interrupted cicatrix on lateral surface. Telson (Figure 2*B*) armed with two pairs of small, movable spines; pair of fixed spines long, extending about midlength of terminal portion (Figure 2*C*); terminal portion hastate, convex dorsally, its length about 7 times basal width. Mesial ramus of uropod overreaching apex of telson by as much as 0.15 its own length; lateral ramus exceeding mesial one by as much as 0.3 its own length.

Petasma (Figure 4*A*, *B*) with dorsomedian lobule produced in relatively broad distomedian projection, bearing elongate distal plate and subtriangular proximal plate raised mesially in strong crest; rib of dorsolateral lobule terminat-

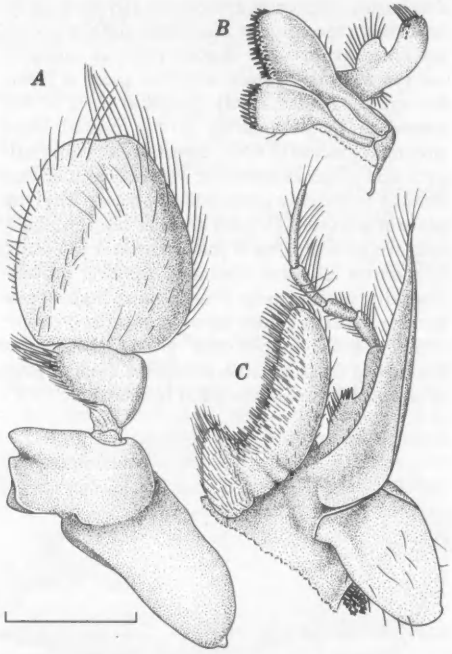

FIGURE 3.—*Penaeopsis balssi*, ♀ 38.5 mm cl, off Natal, South Africa. *A*, Mandible. *B*, First maxilla. *C*, First maxilliped (all from left side). Scale = 5 mm.

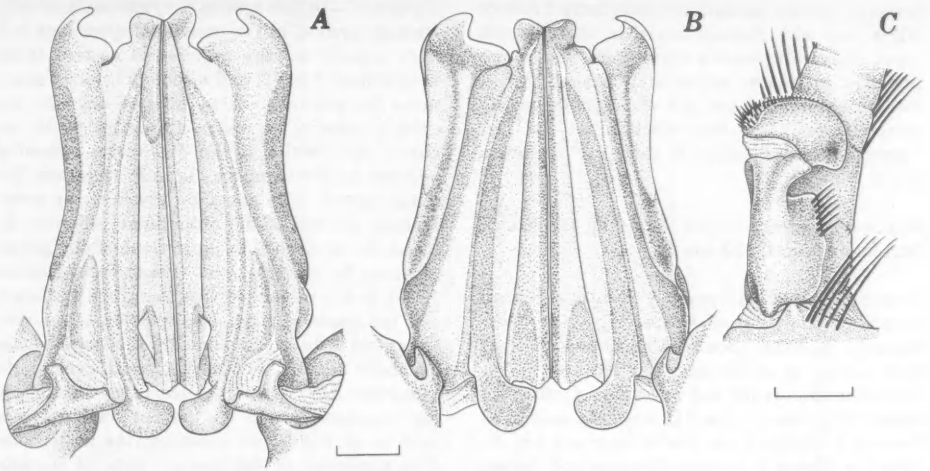

FIGURE 4.—*Penaeopsis balssi*, ♂ 25 mm cl, off Kunduchi, 20 km N of Dar es Salaam. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scales = 1 mm.

ing proximally in flattened, mesially directed suboval process. Ventrolateral lobule with distolateral portion broadly rounded, its rather flexible marginal part broad (extending beyond level of tip of ventral costa) and slightly reflexed inwardly; distal part of ventral costa curving dorsomesially and ending in conspicuous, subsemicircular process (free from, though closely appressed to, margin of dorsolateral lobule) reaching about level of cincinnuli.

Appendix masculina (Figure 4*C*) transversely oval, about twice as broad as long, dorsally convex but for lateral depression, and bearing mesial patch of long setae continuing as increasingly narrower band of shorter setae along distal margin.

Thelycum (Figure 5) with anterior border of plate of sternite XIV posterolaterally inclined, plate produced into paired rather elongate, small lobules flanking posteromedian projection of sternite XIII, almost flat to distinctly convex ventrolaterally, and abruptly slanting dorsomesially toward deep, usually broad, submedian depressions flanking median ridge; latter broad and most prominent basally, tapering and becoming low anteriorly, sometimes reduced to short basal protuberance; lateral portions of sternite XIV densely studded with long setae, row of similar ones extending along anterior border of thoracic ridge, and others forming patch at base of median ridge. Median plate of sternite XIII subtriangular to orbicular, densely studded with long setae radiating from naked central depression; posteromedian projection broad, subrectangular, with

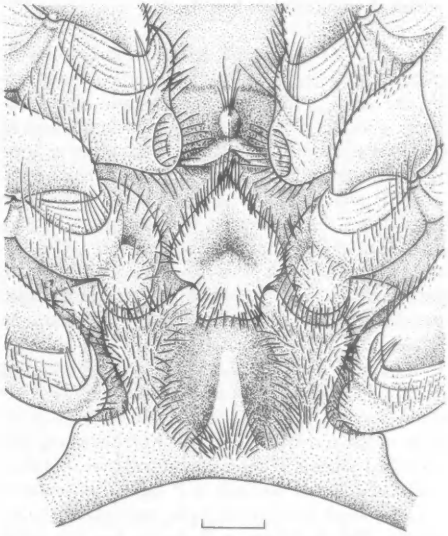

FIGURE 5.—*Penaeopsis balssi*, ♀ 21 mm cl, off Formosa Bay, Kenya, Thelycum ventral view. Scale = 1 mm.

posterior margin straight or emarginate. Sternite XII armed with posteromedian subconical tooth (apex slightly displaced anteriorly and sometimes produced in slender spine) and bearing narrow median carina; oblique pair of ridges extending posterolaterally from base of tooth.

Spermatophore similar to that of *P. rectacuta* (see p. 746).

Maximum lengths.—Males 30 mm cl, 128 mm tl; females 37 mm cl, 150 mm tl.

Geographic and bathymetric ranges.—Indian Ocean, off the coast of Africa (Figure 6), from Somalia to Natal, South Africa, and also off Madagascar, at depths between 280 and 977 m (northernmost record and maximum depth from Balss 1925). The records of this species, as well as those of *P. jerryi,* from Madagascar are not included in Figure 6, because Crosnier and Jouannic (1973) reported the occurrence of these shrimps and their bathymetric ranges in the surrounding waters, but did not cite the localities at which they have been found.

Affinities.—*Penaeopsis balssi* can be distinguished readily from other members of the genus by the usually strongly arcuate and short rostrum, which in adults does not surpass midlength of the second antennular article; in the other species it is straight, slightly sinuous or only somewhat arched, and overreaches the second article or often even the peduncle. The structure of the genitalia in *P. balssi* is closer to that of *P. rectacuta* than to those of its other congeners. In the petasma of *P. balssi,* however, the rather flexible, distolateral part of the ventrolateral lobule is broad, and the ventral costa terminates apically in a broad, nearly rounded process, whereas in that of *P. rectacuta* the distolateral part is relatively narrow, and the ventral costa terminates in a much narrower process. Furthermore, the proximal process of the dorsolateral lobule is suboval and directed mesially in *P. balssi,* whereas in *P. rectacuta* it is nearly circular and extends proximally. The thelycum in *P. balssi* has the plate of sternite XIV flat to strongly convex laterally instead of slanting directly from the border as it does in *P. rectacuta,* and its median ridge is more prominent caudally than in the latter species. These two shrimps differ also by the anteroventral angle of the carapace, about 90° in the latter and obtuse in *P. balssi.*

Variation.—In this species the rostrum is usually strongly arched, but in occasional specimens it is only sightly so; the number of rostral teeth ranges from 8 to 12, and although in most specimens the second tooth is situated opposite the orbital margin, in some, the third tooth occupies this position so that two teeth, instead of one, are on the carapace. As in *P. rectacuta,* the scaphocerite falls short of, reaches, or overreaches the end of the antennular peduncle. In males the distomedian projections of the petasma may be asymmetrical (Ivanov and Hassan 1976), and in some their free margin is scalloped; also the rounded distolateral portion of the ventrolateral lobule occasionally is conspicuously expanded distally. In females, the thelycal plate of sternite XIV varies from nearly flat to strongly convex laterally, and the median ridge may extend to, or end before reaching, the posteromedian projection of the median plate of sternite XIII; the latter plate may be subtriangular, cordiform, or orbicular, and its projection has the caudal margin either straight or shallowly emarginate; also, the posteromedian tooth of sternite XII, often low conical, may be produced into a rather long apical spine directed anteriorly.

Remarks.—According to Boris G. Ivanov (see footnote 2) the coordinates provided by Ivanov and Hassan (1976) for *Van Gogh* stn 34, where two female and two male paratypes were obtained, were incorrect, that the latitude should have been cited as 25°23′ S instead of 23°23′ S.

Ramadan (1938) illustrated the thelyca of an adult and two juveniles in different stages of development. In the juveniles, the submesial depressions are represented by paired pits, and the median plate of sternite XIII is well defined and produced into a sharp, slender, apical spine. This latter feature is not included in Ramadan's illustrations but was observed by me during the examination of the juveniles available to Ramadan, which range in size from 8 to 12 mm cl.

Penaeopsis challengeri De Man 1911

Figures 6-10

Penaeus serratus Bate 1881:182 [lectotype, by present action, ♀, BMNH 1978.323; type-locality, off Matuku, Fiji Is., 19°09′35″ S. 179°41′50″ E, 315 fathoms (576 m), *Challenger* stn 173]; 1888:268 [part], pl. 37,

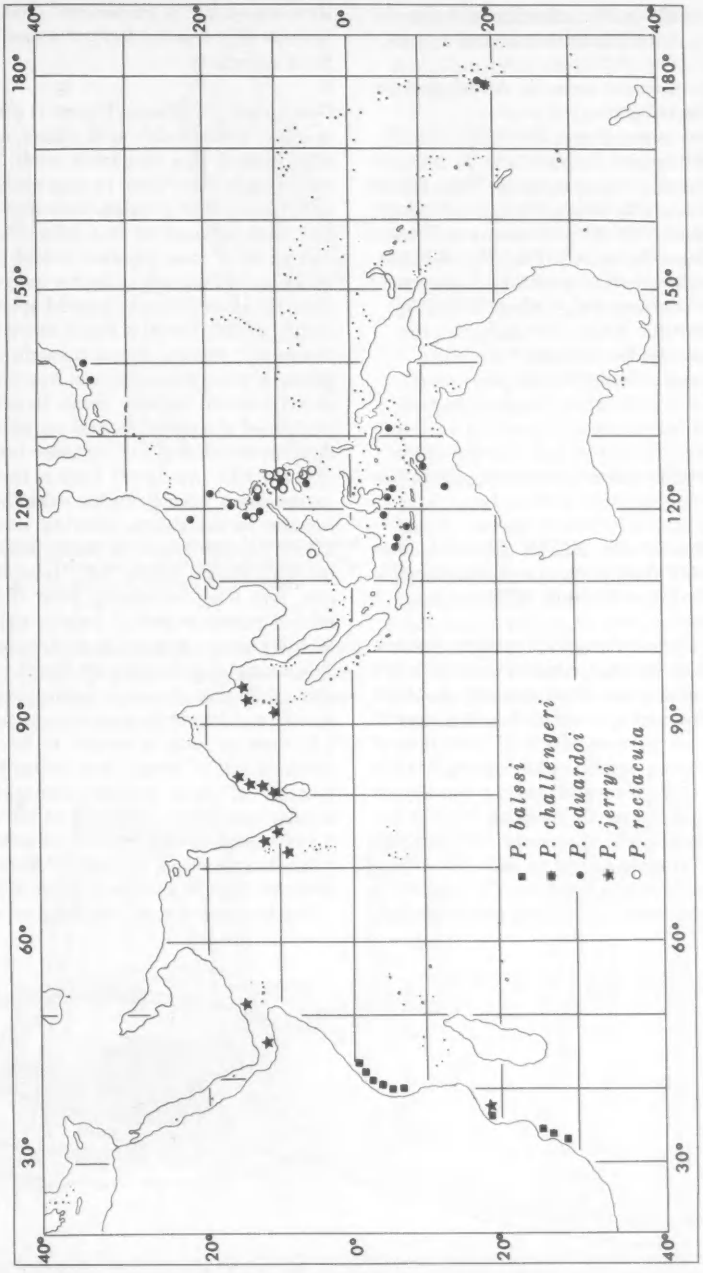

FIGURE 6.—Ranges of *Penaeopsis balssi*, *P. challengeri*, *P. eduardoi*, *P. jerryi*, and *P. rectacuta* based on published records and specimens personally examined.

fig. 1, 1a-b, 1‴, 1z, 1br. Alcock and Anderson 1899:278. A Milne Edwards and Bouvier 1909:225.

Penaeus (Metapenaeus) serratus. Alcock and Anderson 1894:145.

Parapeneus serratus. Alcock 1905:520; 1906:52.

Penaeopsis challengeri De Man 1911:76 [part, replacement name only; not female from Siboga Expedition stn 253, which belongs to *P. eduardoi*]. Schmitt 1926:325. Ivanov and Hassan 1976:4. Pérez Farfante 1977b:173; 1979:208.

Penaeopsis (Penaeopsis) serratus. Burkenroad 1934a:8. Anderson and Lindner 1945:309.

Penaeopsis serratus. Kubo 1949:322.

Penaeopsis serrata. Burukovsky 1974:31.

Not *Penaeopsis serratus* Bate 1881.

Material.

Bate's syntypic series—Lectotype. Paralectotypes:

Fiji Islands—1♂ 3♀, BMNH 1978.324, from type-locality (1♂ from syntypic series assigned to *P. eduardoi* by Pérez Farfante 1977b).

Diagnosis.—Rostrum slightly arched. Anteroventral angle of carapace obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa bearing flexible distolateral projection and ending distally in moderately long spine, not reaching level of cincinnuli. Thelycal plate of sternite XIV with anterior border strongly arched on each side of posteromedian projection of sternite XIII, raised in submesial elevations, and bearing posteromedian subrectangular protuberance (sometimes continuous with depressed ridge) armed with median tooth anteriorly.

Description.—Rostrum (Figure 7) slightly arched in adult, considerably so in young, and deep basally. Rostral plus epigastric teeth 12 (12 or 13 according to Bate 1888) in single specimen available (male) with rostrum unbroken, second rostral tooth situated in line with orbital margin, rostral teeth close together except for more anterior ones. Postrostral carina extending posteriorly for short distance beyond epigastric tooth, ending at about level of dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine relatively small; hepatic spine larger than, and positioned distinctly ventral to, antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 8A). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sharp, slanting sinuously from below hepatic spine to pterygostomian spine; branchiocardiac carina very conspicuous, sinuous, and long, extending from short distance behind posterior end of hepatic sulcus posterodorsally almost to margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.5 times as long as second in former and 1.3 times in latter; prosartema extending to distal margin of first article; distolateral spine slender and sharp, reaching as far as proximal 0.4 of second article; stylocerite ending in small spine, length about 0.4 that of first article. Antennular flagella similar to those of *P. rectacuta*.

Scaphocerite almost reaching or slightly sur-

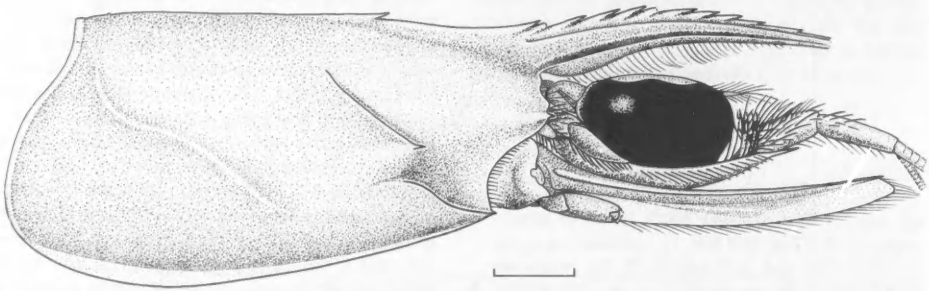

FIGURE 7.—*Penaeopsis challengeri*, lectotype ♀ 24.5 mm cl, off Matuku, Fiji Islands. Cephalothorax, lateral view. Scale = 5 mm.

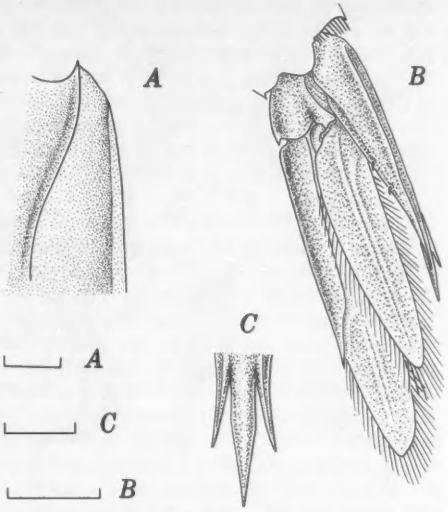

FIGURE 8.—*Penaeopsis challengeri*, lectotype. *A*, Anteroventral part of carapace. *B*, Telson and right uropod, lateral view. *C*, Tip of telson, dorsal view. Scales: *A*, *C* = 2 mm; *B* = 5 mm.

passing distal end of antennular peduncle; lateral rib ending in sharp spine falling short of distal margin of lamella. Antennal flagellum incomplete in available specimens.

Third maxilliped reaching between distal 0.4 of second article and proximal 0.3 of third; ratio of dactyl/propodus about 0.65 in males and 0.75 in females.

First pereopod surpassing carpocerite by half to entire length of dactyl, armed with distomesial spine on basis and ischium. Second pereopod overreaching carpocerite by length of propodus and 0.2 that of carpus (also reaching distal end of first antennular article), with basis and ischium unarmed. Fourth pereopod overreaching carpocerite by length of dactyl and 0.2 that of propodus. Remaining pereopods broken in specimens studied.

Abdomen with sixth somite elongate, about 1.7 times as long as maximum height, bearing barely distinct cicatrix on lateral surface. Telson (Figure 8*B*) with lateral margins armed with two pairs of small movable spines; pair of fixed spines (Figure 8*C*) long, extending as far as base of distal third of terminal portion; terminal portion hastate, distinctly convex dorsally, its length about 5 times basal width. Mesial ramus of uropod slightly overreaching apex of telson (Bate 1888) or overreaching it by as much as 0.2 of its own length, and lateral ramus, in turn, surpassing mesial by as much as 0.3 of its own length.

Petasma (Figure 9*A*, *B*) with dorsomedian lobule produced into well-defined distomedian projection, and bearing small distal plate and

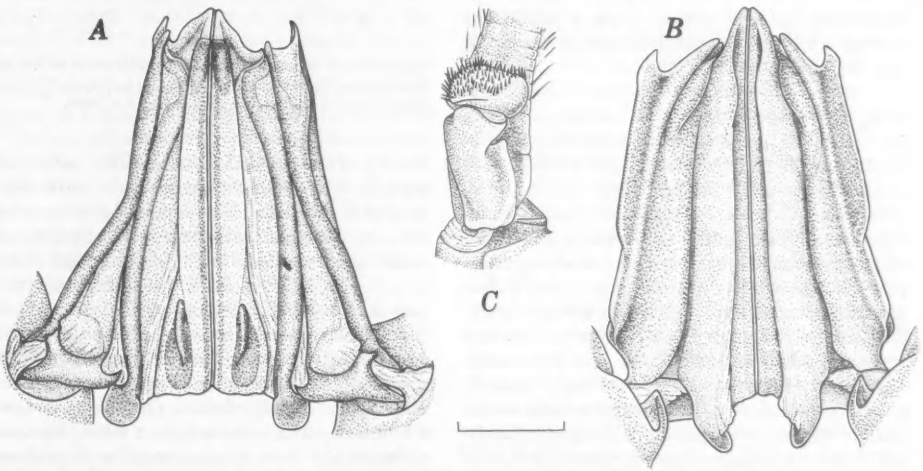

FIGURE 9.—*Penaeopsis challengeri*, ♂ 19 mm cl, off Matuku, Fiji Islands. *A*, Petasma, dorsal view. *B*, Ventral view of same. *C*, Right appendix masculina, dorsal view. Scale = 1 mm.

much larger proximal one, latter raised mesially in conspicuous crest; rib of dorsolateral lobule terminating proximally in subcircular process. Ventrolateral lobule bearing flexible, roughly triangular, subterminal projection distolaterally; ventral costa continuing beyond projection, curving gently dorsomesially, and forming moderately long blunt spine (free from, although closely appressed to, margin of dorsolateral lobule), not reaching level of row of cincinnuli.

Appendix masculina (Figure 9*C*) transversely oval (considerably broader than long), strongly convex dorsally, and with about two-thirds of dorsal surface covered with short setae.

Thelycum (Figure 10*A, B*) with anterior border of plate of sternite XIV strongly arched (delimiting broad lobes) on each side of posteromedian projection of sternite XIII, and bearing long setae, latter also present along lateral borders; plate raised in paired submesial elevations separated anteriorly by deep depression, sometimes interrupted by low median ridge, and bearing posteromedian, strong, subrectangular protuberance armed with anterior, compressed tooth. Median plate of sternite XIII roughly pentagonal, setose, bearing central depression continous with median groove reaching, or almost reaching, apex; posteromedian projection short, with posterior margin entire, Sternite XII armed with small subconical, posteromedian tooth and oblique paired ridges across posterior border.

Maximum lengths.—Only male available, a juvenile 14 mm cl, 65 mm tl; lectotypic female, 24 mm cl, 114 mm tl.

Geographic and bathymetric ranges.—Known only from the type-locality, off Matuku, Fiji Islands, (lat. 19°09′35″ S, long. 179°41′50″ E), 576 m, *Challenger* stn 173 (Figure 6).

Affinities.—The affinities of *P. challengeri* and *P. balssi* are evident in the rostrum, which in both is arched (although considerably more so in the latter) and deep basally, and in the telsonic armature, which consists of two pairs of movable spines in addition to the fixed pair. *Penaeopsis challengeri,* however, differs strikingly from *P. balssi*, as well as from its other congeners, in the unique structure of the external genitalia. In males of *P. challengeri* the ventrolateral lobule of the petasma bears a flexible, roughly triangular process which does not extend beyond the level of the tip of the ventral costa, and the latter ends distally in a spine similar to, but shorter than, that of *P. eduardoi.* The proximal process of the rib of the dorsolateral lobule is subcircular in *P. challengeri* like that in *P. eduardoi* and *P. rectacuta*, but different from the transversely oval one in *P. balssi.* In females of *P. challengeri* the plate of sternite XIV is produced in paired, broad anterior lobes, is raised ventrally in a pair of longitudinal, submesial elevations, and bears a subrectangular posteromedian protuberance sometimes continuing anteriorly as a weak, depressed ridge. In the other species the plate, if produced, forms only small anterior lobes, is flat or (in *P. balssi*) raised in lateral, rather than submesial,

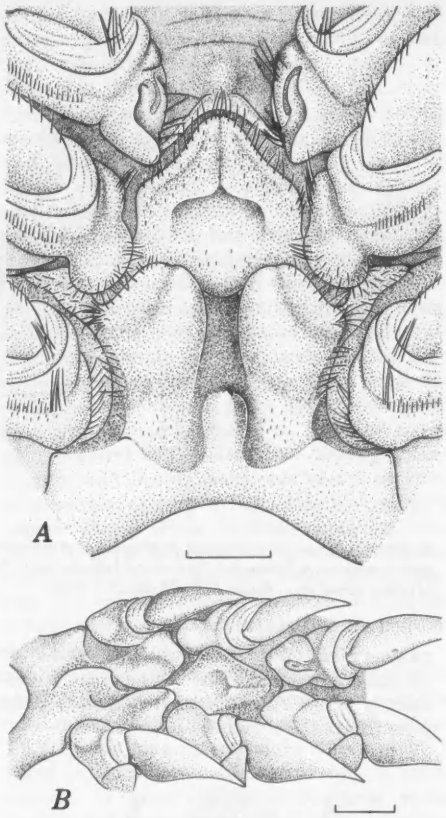

FIGURE 10.—*Penaeopsis challengeri. A,* ♀ 22 mm cl, off Matuku, Fiji Islands. Thelycum, ventral view. *B,* Lectotype. Thelycum, ventrolateral view (setae not shown). Scales = 1 mm.

elevations, and the posteromedian protuberance is caudally pedunculate in *P. eduardoi* (in the other species a strong median ridge instead of a protuberance is usually present). Finally, in *P. challengeri* the median plate of sternite XIII is subpentagonal instead of semicircular or cordiform and exhibits a central depression which continues anteriorly as a median groove.

Remarks.–As Pérez Farfante (1977b) pointed out, Bate (1888) illustrated the petasma of a male of his *Penaeus serratus* [= *Penaeopsis challengeri*] that actually belongs to a different species, *Penaeopsis eduardoi*. This male together with nine females and at least one other male were taken of Matuku, Fiji Islands, at *Challenger* stn 173. Five of these females were identified by Bate as *Penaeus rectacutus* [they are actually, at least the three that are now in the BMNH, *Penaeopsis eduardoi*], the other four females are syntypes of his *Penaeus serratus*, and the male must be assumed to be a member of the syntypic series. It is beyond question that the male depicted by Bate as *P. serratus* is a specimen of *Penaeopsis eduardoi*: the dorsomedian projections of the petasma are obsolete and each ventral costa is produced in a long spine extending considerably farther distodorsally than that in *Penaeus serratus*. The probability that Bate also examined the syntypic second male (which is *P. serratus*, 65 mm tl) is indicated by his statement "Length . . . of the largest male 76 mm"; this clearly indicates that he had at least one other male in addition to the "largest" one. The smaller male was in the jar with the three females of "*Penaeus rectacutus*" [= *Penaeopsis eduardoi*], but Bate mentioned no male of this species whereas he referred to males of *Penaeus serratus;* consequently, it seems most likely that the small male *P. serratus* was mistakingly placed with the three females of the former species. In regard to the number of male specimens recognized by Bate as "*Penaeus serratus*," it should be mentioned that Alcock and Anderson (1899) stated that "there are two *Challenger* specimens [of *P. serratus*] from Fiji in the Indian Museum" and it is possible that one of them is a male that was examined by Bate.

Inasmuch as the type-material of *P. serratus* Bate included a second species, *Penaeopsis eduardoi*, and a holotype was not designated, it is desirable to select one specimen as the lectotype to associate the name with the species to which it is applied. Although Bate (1888:269) mentioned the "type" of *Penaeus serratus*, there is no indication as to which specimen he was referring; however, he stated that some specimens taken off the Fiji Islands "were placed under *Penaeus rectacutus* because the thelycum corresponds with that species rather than with the type of this [*Penaeus serratus*]." His statement leaves no doubt that it was a female to which he was referring. Because the first specimen specifically cited by him (p. 268) was the "largest female, 114 mm" [24 mm cl], I have selected it as the lectotype of *Penaeus serratus* Bate 1881. This specimen has been assigned BMNH 1978.323.

The very young specimen (a female) taken in the Torres Strait, at *Challenger* stn 184, which Bate (1888) recorded as "*Penaeus serratus*," is actually a member of the genus *Metapenaeopsis*, *M. sinuosa* Dall 1957, or a closely related species.

In the last 45 yr various authors (Burkenroad 1934a; Kubo 1949; Ivanov and Hassan 1976) have pointed out the difficulty in defining the specific characters of "*Penaeus serratus*." The uncertainty was due to Bate's (1881) imprecise original diagnosis and the inadequate, although rather elaborate, description, accompanied by figures lacking detail (e.g., a sketchy one of the thelycum and incomplete representations of the telson which is depicted as lacking movable spines), that was subsequently presented by him (1888). I have studied part of the type-series and offer a new description and illustrations of those specimens, including the only available description of the petasma.

Penaeopsis challengeri, like all of its congeners except *P. rectacuta* and *P. jerryi*, possesses only two pairs of movable spines on the telson. This character was noted by Bate (1888); however, in discussing the relationships of *P. eduardoi* with other members of *Penaeopsis*, I (1977b) erroneously stated that *P. challengeri* exhibits three pairs of movable telsonic spines. The specimens examined by me at the time were the four female syntypes in only one of which the telson is entire, but it had been bent and torn in such a way that its sharp edge projected laterally in what appeared to be a pair of minute movable spines. My confirmation of Bate's observation on the spination of the telson has been based on a reexamination of the just mentioned female, and a study of the male which, although caught together with the four female syntypes of "*Penaeus serratus*," was not explicitly cited by him.

Alcock and Anderson (1899) concluded that "*P.*

serratus" [= *P. challengeri*] lacks an epipod on somite XII (third pereopod), whereas *P. rectacuta* has one. This observation is in error; not only both of these species possess such an epipod, but also its presence is typical of all members of the genus.

Penaeopsis eduardoi Pérez Farfante 1977

Figures 6, 11-14

Penaeus rectacutus. Bate 1888:266 [part], pl. 36, fig. 2z. ? Villaluz and Arriola 1938:38, pl. 3, fig. 3.

Penaeus serratus. Bate 1888:268 [part], pl. 37, fig. 1", 1q.

Parapenaeus rectacutus. De Man 1911:82; 1913, pl. 8, fig. 26a-c. Yokoya 1933:9.

Penaeopsis rectactus. Kubo 1949:322, fig. 1H; 8J; 19C; 23A-B; 36K-L; 47J; 58P; 76A, F; 78K; 118 A-E, [?F], G; 119.

Penaeopsis challengeri. De Man 1911:76 [part, ♀ from Siboga-Expedition stn 253]. Ivanov and Hassan 1976:4.

Penaeopsis rectacutus. Burukovsky 1974:31, fig. 37a-c.

Penaeopsis eduardoi Pérez Farfante 1977b:172, fig. 1-4 [holotype, ♀, USNM 168298; type-locality, Balayan Bay, Luzon I., Philippines, 13°41'00" N, 120°47'05" E, 366 m, *Albatross* stn 5116]. Pérez Farfante 1979:208.

Not *Penaeus rectacutus* Bate 1881, or *Penaeus serratus* Bate 1881, or *Penaeopsis challengeri* De Man 1911.

Material.—For list of records see Pérez Farfante 1977b. Additional records are:

PHILIPPINES—1♂, USNM, W of Cabo Engaño, N Luzon, 410 m, 12 November 1908, *Albatross* stn 5325. 3♀, USNM, W of San Fernando Pt, Luzon, 315 m, 10 May 1909, *Albatross* stn 5440. 9♂ 8♀, USNM, Balayan Bay, Luzon, 366 m, 20 January 1908, *Albatross* stn 5116. 1♀, VNIRO, Burias Pass, Sibuyan Sea, 400 m, 1 June 1973, *Lira* haul 71. 1♂, USNM, off Calapan, Mindoro I, 198 m, 2 February 1908, *Albatross* stn 5121. 2♂ 1♀, USNM, Macajalar Bay, Mindanao, 479 m, 5 August 1909, *Albatross* stn 5506.

INDONESIA—1♀, USNM, off Tanakeke I, Flores Sea, 386 m, 21 December 1909, *Albatross* stn 5662. 1♀, VNIRO, S of Roti I, Timor Sea, 400 m, 1 June 1973, *Lira*, O. A. Petrov. 1♂ 2♀, VNIRO, S of Timor I, Timor Sea, 320-355 m, 5 May 1973, *Lira*, O. A. Petrov.

Diagnosis.—Rostrum straight or sinuous, and long, reaching or overreaching third antennular article. Anteroventral angle of carapace broadly obtuse. Telson with two pairs of movable spines. Petasma with proximal plate of dorsomedian lobule lacking mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa lacking distolateral projection and ending distally in long spine extending beyond level of row of cincinnuli. Thelycal plate of sternite XIV with anterior border weakly to distinctly arched on each side of posteromedian projection of sternite XIII and strongly sloping posterolaterally; lateral borders turning mesially behind midlength, then posteriorly; short posteromedian protuberance caudally pedunculate.

Description.—Rostrum (Figure 11) horizontal or somewhat upturned, straight or slightly sinuous (strongly arched in young), and long, reaching at least midlength of third antennular article and often overreaching peduncle, its length ranging from about 0.7 to 0.9 that of carapace. Rostral

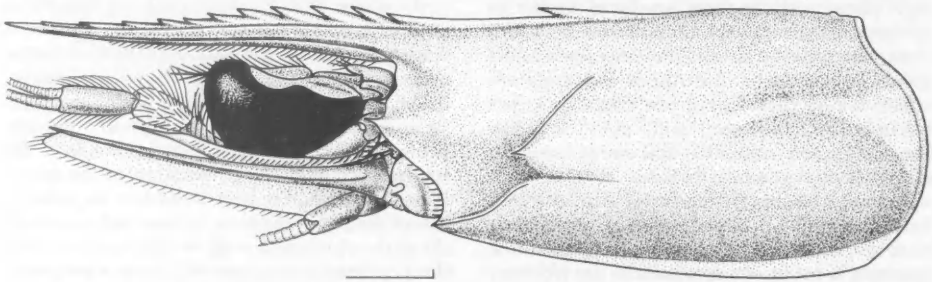

FIGURE 11.—*Penaeopsis eduardoi*, holotype ♀ 27 mm cl, Balayan Bay, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5 mm.

plus epigastric teeth 8-15, basal rostral teeth close together, ultimate 3 or 4 usually relatively widely spaced; first rostral tooth situated in line with orbital margin. Postrostral carina low, although well defined, behind epigastric tooth, ending at about posterior 0.4 length of carapace, beyond level of dorsal extremity of cervical sulcus; small dorsal tubercle located near posterior margin of carapace. Antennal and hepatic spines subequal in size, latter situated distinctly ventral to antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 12A). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sigmoid anteriorly (from below hepatic spine to apex of ptergostomian spine), hepatic sulcus well marked along carina, very shallow posteriorly. Branchiocardiac carina, extending well behind hepatic sulcus posterodorsally to near margin of carapace, indistinct in many large individuals.

Antennular peduncle with length equivalent to about 0.65 that of carapace, third article stouter and longer in male than in female, about 1.50 as long as second in former and 1.25 in latter; prosartema not quite reaching distal margin of first article; distolateral spine long, slender, and sharp, reaching between basal 0.65 and distal margin of second article; stylocerite ending in small spine, length about 0.4 that of first article. Flagella similar to those of *P. rectacuta*, but ventral flagellum in male with less conspicuous knob at junction between semicircular proximal part and straight distal part.

Scaphocerite extending to, or barely surpassing, antennular peduncle; lateral rib ending in sharp spine ending slightly short of distal margin of lamella. Antennal flagellum broken in specimens examined, but not <2.5 as long as body.

Third maxilliped of male extending as far as distal 0.35 of third antennular article, that of female to distal margin; ratio of dactyl/propodus about 0.70 in male and 0.75 in female.

First pereopod extending to about distal end of carpocerite. Second pereopod overreaching carpocerite by length of dactyl or by almost entire propodus (i.e., reaching at least distal 0.4, at most 0.1, of first antennular article). Third pereopod of male reaching between proximal 0.35 and distal end of second article, that of female, between midlength and distal end of third article. Fourth pereopod extending to distal end of carpocerite or surpassing it by length of dactyl. Fifth pereopod reaching at least midlength of second article or slightly overreaching third. Order of pereopods in terms of their maximum anterior extensions: first, fourth, second, third, and fifth (or fifth, and third). Third maxilliped reaching about as far as fifth pereopod.

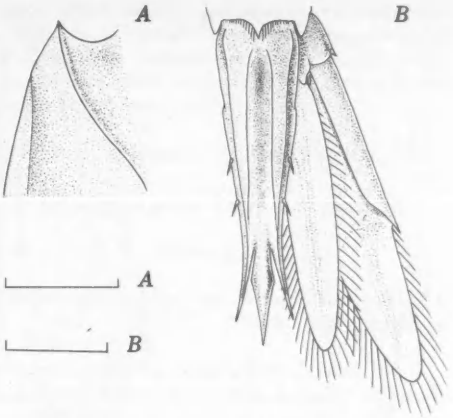

FIGURE 12.—*Penaeopsis eduardoi*, holotype. *A*, Anteroventral part of carapace. *B*, Telson and right uropod, dorsal view. Scales = 5 mm.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing rather strong, usually interrupted cicatrix on lateral surface. Telson (Figure 12*B*) with lateral margins armed with two pairs of small, movable spines; pair of fixed spines very long, in young reaching level of apex of telson; terminal portion hastate, its length 6-7 times basal width. Mesial ramus of uropod reaching, or slightly overreaching, apex of telson; lateral ramus surpassing mesial one by almost 0.2 of its own length.

Petasma (Figure 13*A*, *B*) with distomedian projection virtually obsolete, distal plate relatively broad, and proximal plate flush with surrounding membranous portion, lacking mesial crest. Rib of dorsolateral lobule terminating proximally in subcircular process. Ventral costa with distolateral portion situated marginally (where bent inward), curving rather gently at about 120° and continuing in long spine distodorsally beyond row of cincinnuli.

Appendix masculina (Figure 13*C*) transversely oval, broader than long, width 1.35-1.60 length, strongly convex dorsally, and bearing short setae around entire margin.

Thelycum (Figure 14) with anterior border of

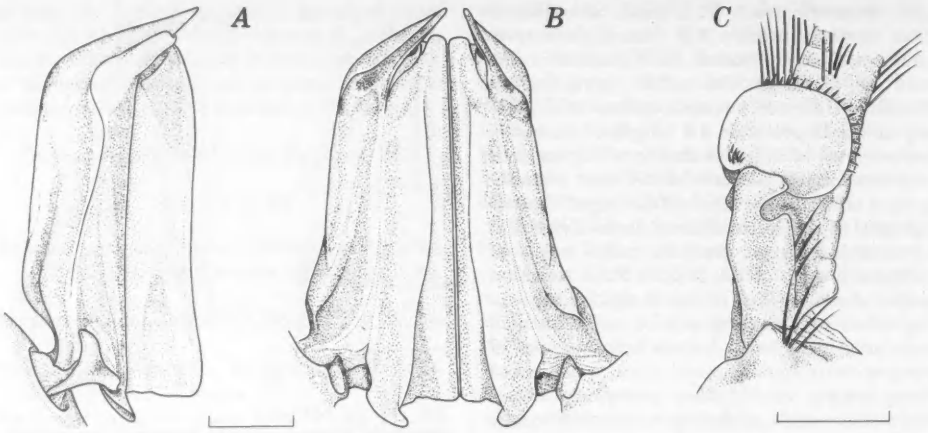

FIGURE 13.—*Penaeopsis eduardoi*, ♂ 16.5 mm cl, off Matuku, Fiji Islands. *A*, Petasma, lateral view of left half. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scales = 1 mm.

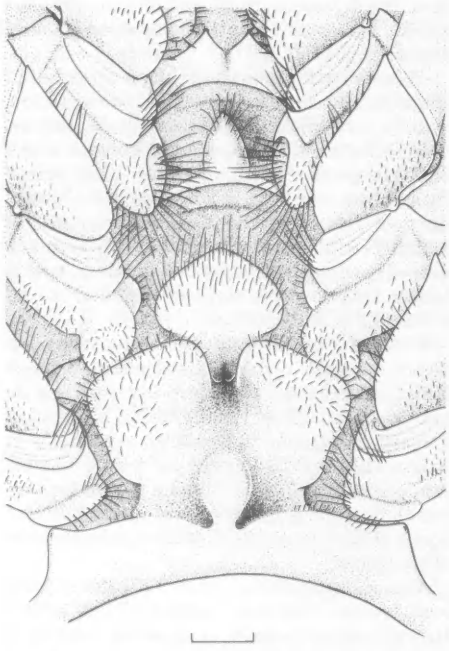

FIGURE 14.—*Penaeopsis eduardoi*, holotype. Thelycum, ventral view. Scale = 1 mm.

plate of sternite XIV faintly to distinctly convex on each side of posteromedian projection of sternite XIII, and conspicuously sloping posterolaterally; lateral borders sharply turning mesially behind midlength then posteriorly before joining posterior thoracic ridge; plate densely setose anteriorly, strongly slanting dorsomesially toward deep anteromedian portion, and armed with short, caudally pedunculate posteromedian protuberance. Median plate of sternite XIII semicircular to subcordiform (with blunt apex), flat, covered with setae; posteromedian projection caudally bifurcate. Sternite XII bearing posteromedian, semiconical, broad (rather than compressed) tooth; oblique pair of strong, sharp ridges extending posterolaterally from base of tooth.

Maximum lengths.—Males 26 mm cl, about 114 mm tl; females 34 mm cl, about 130 mm tl.

Geographic and bathymetric ranges.—*Penaeopsis eduardoi* has been found off the Fiji Islands and from Japan through the Philippines and Indonesia to the Timor Sea (Figure 6), in depths between 289 and 570 m.

Previously, Pérez Farfante (1977b) noted that the range of this species extends to the "southwestern part of the Bay of Bengal." In their treatment of "*Metapenaeus rectacutus*" [= *P. jer-*

ryi], Alcock and Anderson (1894) stated (in the account of the deep sea Crustacea collected in the Bay of Bengal and Laccadive Sea by the *Investigator* during the seasons 1891-92 and 1893-94) that they had little hesitation in identifying the females with Bate's "*Penaeus rectacutus*," but that the males "appear to agree in every detail . . .with Spence Bate's figures and descriptions of *Penaeus serratus*." Because the male "*Penaeus serratus*" figured by Bate is a member of *Penaeopsis eduardoi*, I assumed that the males available to them belonged to the latter species. On the basis of their statement that "*M. rectacutus*" was common in the Bay of Bengal between 100 and 280 fm (183 and 357 m) and my noting the fact that the stations established by the *Investigator* during the years and within the depth limits cited above were all located in the southwestern part of the Bay of Bengal, I was led to the conclusion that *P. eduardoi* had been found in the latter area. Further studies, together with the fact that no specimen of *P. eduardoi* has been reported west of the Strait of Malacca, have inclined me to believe that Alcock and Anderson probably misidentified the males of "*Metapenaeus rectacutus*" [= *Penaeopsis jerryi*] as "*Penaeus serratus*" [= *Penaeopsis eduardoi*]. It should be added that the specimens of "*M. rectacutus*" examined by the later authors are no longer extant (G. Ramakrishna[3]).

Affinities.—*Penaeopsis eduardoi* differs from *P. rectacuta* and *P. jerryi* in possessing two pairs of movable spines on the telson, a character it shares with two other Indo-West Pacific species, *P. challengeri* and *P. balssi*, as well as with the amphi-Atlantic *P. serrata*. *Penaeopsis eduardoi*, however, can be distinguished from all its congeners by features of the petasma and thelycum. It is the only species in which the distomedian projections of the petasma are obsolete, the proximal plate lacks mesial crest, and the ventral costa is produced in a long, distal spine extending beyond the row of cincinnuli. The thelycum, in turn, is unique in that the plate of sternite XIV exhibits a caudally pedunculate posteromedian protuberance, whereas in all the other species the latter is represented by a ridge or protuberance which is broad caudally or lacks a peduncle. Furthermore, sternite XII is armed with an elongate, broad basally, semiconical, anteriorly directed tooth, which in the other members of *Penaeopsis* is indistinct or either laterally compressed, or short, subconical and directed ventrally or anteroventrally.

Variation.—Discussed by Pérez Farfante 1977b.

Penaeopsis jerryi Pérez Farfante 1979

Figures 6, 15-19

Metapenaeus rectacutus. Wood-Mason 1891:274. Alcock 1901b:50. Alcock and Anderson 1894:145.

Peneus rectacutus. Alcock 1898:73.

Penaeus rectacutus. Alcock and Anderson 1899:278.

Peneus (Parapeneus) rectacutus. Alcock 1901a:17 Alcock and McArdle 1901, pl. 49, fig. 5.

Parapeneus rectacutus. Alcock 1902:268, fig. 62; 1905:520 [part]; 1906:33, pl. 6, fig. 19, 19a-b. Kemp and Sewell 1912:16. ?Balss 1925:228.

Parapenaeus rectacutus. Schmitt 1926:319.

Penaeopsis rectacutus. Schmitt 1926:321. Ramadan 1938:67, fig. 12a-b. Sewell 1955:202. Kurian 1964:216.

Penaeopsis rectacuta. Holthuis and Rosa 1965:3 [part]. George 1966:342. Jones 1967:1337; 1969:747. George 1969:27. Longhurst 1971:224. Starobogatov 1972:390 [key, but not figures]. Crosnier and Jouannic 1973:12, pl. 3, fig. 3. Ivanov and Hassan 1976:5, fig. 3.

Penaeopsis jerryi Pérez Farfante 1979:208, fig. 1-4 [holotype, ♀, BNMH 1978:325; type-locality: off Berbera, Somalia, Gulf of Aden, 10°29′48″ N, 45°01′48″ E, John Murray Expedition stn 16].

Not *Penaeus rectacutus* Bate 1881.

Material.

Holotype. Paratypes:

YEMEN—2♂ 2♀, USNM 171430, off Saihut (15°10′ N, 50°58′ E), 240-239 m, 16 May 1971, A. D. Druzhinin.

SOMALIA—20♂ 49♀, BMNH 1978.326, collected with holotype.

INDIA—2♂ 2♀, USNM 171431, off Cochin, summer 1978, Staff of the Department of Marine Science, University of Cochin. 1♀, USNM 42755, off False Divi Pt (15°56′50″ N, 81°30′30″ E), 439-505 m, 24 December 1890, *Investigator* stn

[3]G. Ramakrishna, Superintending Zoologist, Zoological Survey of India, pers. commun. 20 March 1978.

120. 2♂ 1♀, ZSI 2589-95/10, N of North Andaman I (14°13′ N, 93°40′ E), 677-766 m, 8 April 1898, *Investigator* stn 235.

Diagnosis.—Rostrum straight or sinuous (occasionally convex basally, straight anteriorly), and long, reaching or overreaching third antennular article. Anteroventral extremity of carapace forming angle of about 90°; hepatic spine located at about same level as that of antennal spine; branchiocardiac carina with anterior end very close to hepatic sulcus. Telson with three pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa ending distally in short, relatively narrow process. Thelycal plate of sternite XIV with anterior border broadly arched on each side of posteromedian protuberance of sternite XIII and strongly inclined posterolaterally; anterolateral and posterolateral corners of plate arched; median ridge broadest and most salient posteriorly, often gradually tapering anteriorly, sometimes reduced to posterior tubercle; median plate of sternite XIII subsemicircular to trilobed.

Description.—Rostrum (Figures 15, 16) almost horizontal, straight or slightly sinuous (occasionally convex basally, straight anteriorly), falling short of to overreaching distal margin of antennular peduncle, its length 0.8-0.9 that of carapace. Rostral plus epigastric teeth 12-16 (usually 12-14), second (occasionally first) rostral tooth situated in line with orbital margin, basal teeth close together, those toward apex more widely spaced, and extending almost to tip of rostrum, but sometimes only to base of anterior 0.2. Postrostral carina extending posteriorly to about level of dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine moderately long; antennal carina short but prominent. Hepatic spine slightly larger than, and situated at about same level as (rather than ventral to), antennal spine. Anteroventral extremity of carapace forming angle of about 90° (Figure 17*A*). Cervical carina sharp, accompanying sulcus well marked; hepatic carina slanting sinuously from below hepatic spine to pterygostomian spine; branchiocardiac carina strong, with anterior extremity almost reaching posterior end of hepatic sulcus and extending posteriorly to near margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in mature male than in

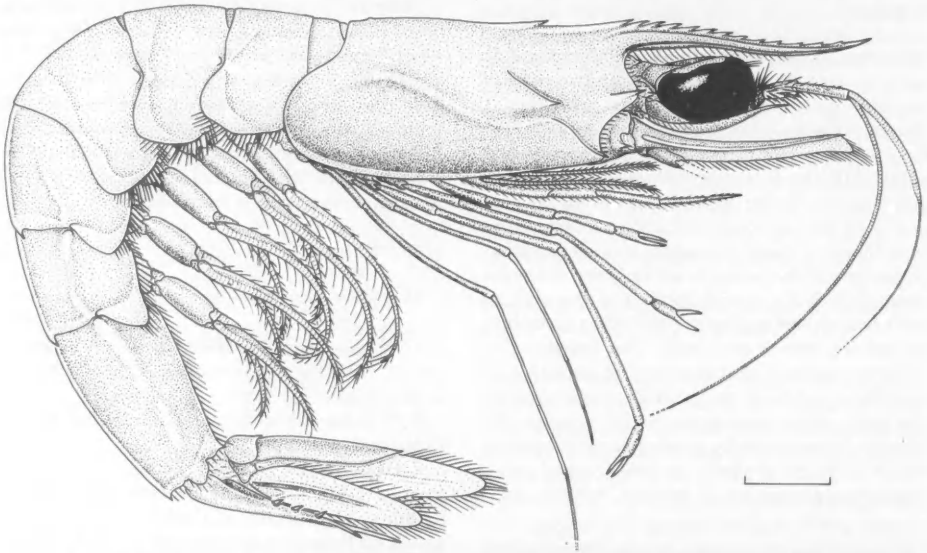

FIGURE 15.—*Penaeopsis jerryi*, ♀ 17.5 mm cl, off Berbera, Gulf of Aden, Somalia. Lateral view. Scale = 5 mm.

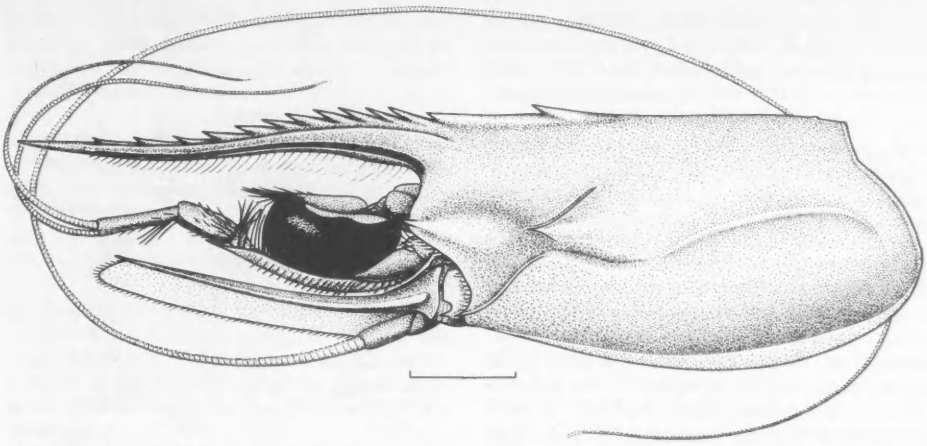

FIGURE 16.—*Penaeopsis jerryi, holotype* ♀ 20.5 mm cl, off Berbera, Gulf of Aden, Somalia. Cephalothorax, lateral view. Scale = 5 mm.

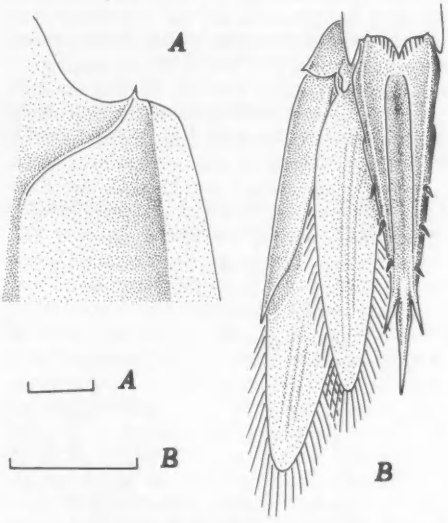

FIGURE 17.—*Penaeopsis jerryi*, holotype. *A*, Anteroventral part of carapace. *B*, Telson and left uropod, dorsal view. Scales: *A* = 2 mm, *B* = 5 mm.

female, about 1.6 times as long as second in former and 1.4 in latter; prosartema almost attaining distal margin of first article; distolateral spine slender, sharp, and reaching about midlength of second article. Flagella similar to those of *P. rectacuta*.

Scaphocerite falling short of to overreaching distal end of antennular peduncle; lateral rib ending in slender spine, falling slightly short of margin of lamella. Antennal flagellum more than twice the length of the animal (Kurian 1964).

Third maxilliped and pereopods in most specimens too poorly preserved to allow observations on their maximum anterior extensions.

Abdomen with sixth somite elongate, about 1.7 times height, bearing long, strong, interrupted cicatrix on lateral surface; cicatrix also on fifth and fourth somites. Telson (Figure 17*B*) with lateral margins bearing three pairs of small, movable spines (occasionally only one or two pairs, rarely with different numbers of spines on margins); fixed spines variable in length, reaching at most base of distal third of terminal portion; terminal portion with length about 6-7 times basal width, narrowly hastate or with lateral margins basally rounded, and dorsal surface moderately convex. Mesial ramus of uropod falling short of to overreaching apex of telson by as much as 0.2 of its own length; lateral ramus overreaching mesial ramus by about 0.2 of its own length.

Petasma (Figure 18*A*, *B*) with dorsomedian lobule produced into rather broad distomedian projection, and bearing elongate distal plate and broader, subtriangular proximal plate raised mesially in blunt crest; rib of dorsolateral lobule with distal part straight or turning laterally, and terminating proximally in semicircular or subcircular process. Ventrolateral lobule bearing

distally rather flexible and translucent marginal region, reflexed inwardly; distal part of ventral costa curving abruptly dorsomesially and ending in short, relatively narrow process reaching approximately to level of cincinnuli.

Appendix masculina (Figure 18*C*) considerably broader than long (width about 1.7 length), roughly oval; band of setae extending around free margin, broadening and forming patch mesially.

Thelycum (Figure 19) with plate of sternite XIV roughly subelliptical in outline, its anterior border strongly arcuate and inclined posterolaterally, and anterolateral and posterolateral corners arched, plate sloping toward submedian depressions of variable length, and bearing long marginal setae; median ridge broadest and most prominent posteriorly, tapering anteriorly, sometimes reduced to posterior tubercle. Posterior thoracic ridge narrow and projecting anteroventrally at base of median ridge, fringed anteriorly with closely set setae. Median plate of sternite XIII subsemicircular to roughly trilobed, sometimes with minute anteromedian spine, and covered with setae except for central depression; posteromedian projection broad, with posterior margin entire or very shallowly emarginate. Sternite XII bearing posteromedian, subconical tooth with apex directed anteroventrally; oblique pairs of sharp ridges extending posterolaterally from base of tooth.

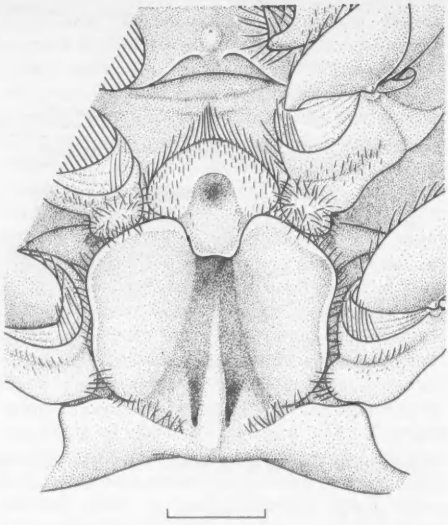

FIGURE 19.—*Penaeopsis jerryi*, holotype. Thelycum ventral view. Scale = 1 mm.

Spermatophore bearing mesial element which in impregnated females lies exposed on the thelycum.

Color.—Red (Wood-Mason 1891), or dark brown with reddish tint (Kurian 1964).

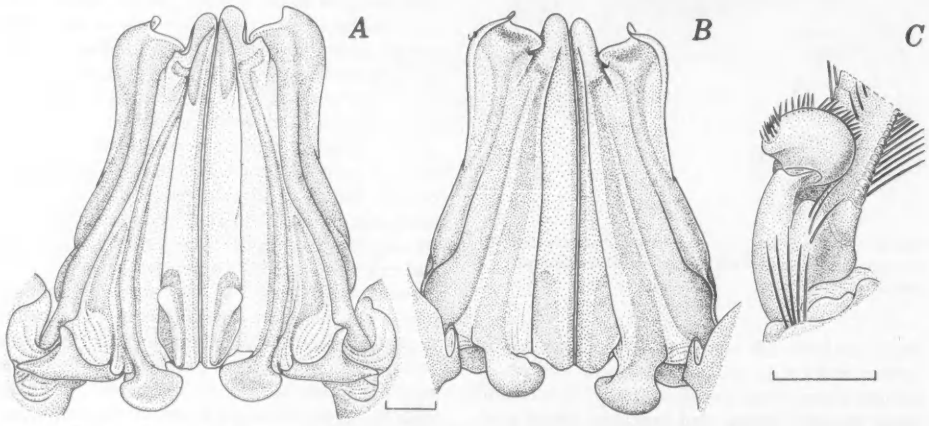

FIGURE 18.—*Penaeopsis jerryi*, ♂ 19 mm cl, of Berbera, Gulf of Aden, Somalia. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Paratype ♂ 21 mm cl, off Cochin, India, right appendix masculina, dorsal view. Scales = 1 mm.

Maximum lengths.—160 mm tl (Crosnier and Jouannic 1973). Largest specimens examined by me: males 23 mm cl, about 107 mm tl; females 33 mm cl, about 138 mm tl.

Geographic and bathymetric ranges.—Indian Ocean (Figure 6), from the Bay of Bengal (Andaman Sea; off Madras) through the Arabian Sea (off Cochin) to the Gulf Aden (off Berbera) and south to off Mozambique and Madagascar. It has been found at depths between 183 and 677 m.

Affinities.—*Penaeopsis jerryi* differs from the closely related *P. rectacuta*, from the South China Sea, Philippines, and Indonesia, mainly by the position of the hepatic spine, the length of the branchiocardiac carina, and features of the thelycum.

In *P. rectacuta* the hepatic spine is located at a level distinctly ventral to, instead of about the same level as, that of the antennal spine, and the branchiocardiac carina ends farther from the hepatic sulcus than it does in *P. jerryi*.

The petasmata of the two species, although similar, differ in that the rib of the dorsolateral lobule in *P. rectacuta* is straight distally and terminates proximally in a subcircular process, whereas in *P. jerryi* the rib sometimes turns laterally and often ends in a semicircular process.

In *P. rectacuta* the thelycal plate of sternite XIV is usually roughly trapezoidal, with the anterior border almost straight on each side of the posteromedian projection of sternite XIII, and the anterolateral corners forming angles, whereas in *P. jerryi* this plate is roughly elliptical with the anterior border arcuate and the anterolateral and posterolateral corners arched. Finally, in *P. jerryi* the median plate of sternite XIII is subsemicircular [e.g., in females illustrated by Alcock (1906, pl. 6: fig. 19a) and by Ivanov and Hassan (1976, fig. 3) as well as in most of those examined by me], or occasionally weakly trilobed as in the specimen figured by Ramadan (1938, fig. 12b). In a few females I have studied, the plate, although almost semicircular, is produced into a minute anteromedian spine, its general shape thus being quite different from the cordiform median plate of *P. rectacuta*.

In occasional specimens of *P. jerryi*, the basis of the second pair of pereopods is armed with a distomesial spine (Alcock 1901a), a feature that has not been observed in the other species. Also, as pointed out by Ramadan (1938) and confirmed by my observation, some individuals bear less than the tree typical pairs of movable spines on the telson (one or two pairs) and I found one with the spination asymmetrical.

Remarks.—On the basis of the scant information provided by Balss (1925) it has not been possible for me to determine the identity of the two females he recorded as "*Parapenaeus rectacutus*" from the Nicobar Islands, Bay of Bengal. According to him, the telson bears two pairs of movable spines, a characteristic of three of the five Indo-West Pacific members of the genus—*Penaeopsis balssi*, *P. challengeri*, and *P. eduardoi*. In the same work, however, he identified specimens belonging to *P. balssi*, which were taken off east Africa, as "?*Penaeopsis challengeri*"; consequently, it seems very unlikely that the two females belong to *P. balssi*. It also seems improbable that they are members of *P. challengeri* or *P. eduardoi* because these species are not known to occur in the Indian Ocean. Balss added that in his specimens the second pair of pereopods is armed with spines; such have been observed only in occasional individuals of *P. jerryi*; but three, not two pairs of movable telsonic spines are characteristic of this shrimp typically. Balss' specimens, however, may prove to be atypical *P. jerryi* because this shrimp is the only species of the genus that has been recorded from the area.

Commercial importance.—Survey fishing off the west coast of India at depths between 175 and 375 m (George 1966, 1969; Jones 1967; Longhurst 1971) demonstrated the presence of *P. jerryi* in sufficient numbers for possible commercial exploitation of this shrimp. Crosnier and Jouannic (1973) noted that this species eventually will become commercially fished off Madagascar.

Penaeopsis rectacuta (Bate 1881)

Figures 6, 20-27

Penaeus rectacutus Bate 1881:180 [♀ holotype, BNMH; type-locality, between Bohol and Cebu, Philippines, 10°14′ N, 123°54′ E, 95 fathoms (174 m), *Challenger* stn 209]; 1888:266 [part], pl. 36, fig. 2, 2″, 2 p [fig. 2z = *P. eduardoi*]. Estampador 1937:493. Domantay 1956:363. Pérez Farfante 1977b:172.

Parapeneus rectacutus. Alcock 1905:520 [part, references only].

Penaeopsis (Penaeopsis) rectacutus. Burkenroad 1934a:5 Anderson and Lindner 1945:309.

Penaeopsis rectacuta. Hall 1962:18, fig. 89, 89a, 89b. Holthuis and Rosa 1965:3 [part]. Starobogatov 1972, pl. 5, fig. 39a-b (figures, but not key). Pérez Farfante 1977b:180; 1979:208.

Common names: needle shrimp; camarón aguja; crevette aiguille.

Material.

PHILIPPINES—Luzon: 5♂ 10♀, USNM, SW of Nasugbu, 247 m, 15 January 1908, *Albatross* stn 5110. 1♀, USNM, Balayan Bay, 324 m, 17 January 1908, *Albatross* stn 5112. 1♂, USNM, Balayan Bay, 366 m, 20 January 1908, *Albatross* stn 5116. 1♀, USNM, off Malabrigo Pt., 198 m, 2 February 1908, *Albatross* stn 5121. 2♂ 1♀, USNM, Tabayas Bay, 274 m, 24 February 1909, *Albatross* stn 5372. 3♀, USNM, Tabayas Bay, 348 m, 2 March 1909, *Albatross* stn 5374. 2♀, USNM, Albay Gulf, 368 m, 8 June 1909 *Albatross* stn 5459.

Leyte: 2♀, USNM, off Palompon, 344 m, 16 March 1909, *Albatross* stn 5402. 10♂ 13♀, USNM, off Palompon, 333 m, 16 March 1909, *Albatross* stn 5403.

Camotes Is: 2♂ 1♀, USNM, Off Pacijan, 291 m, 18 March 1909, *Albatross* stn 5408. 1♀, USNM, off Pacijan, 346 m, 18 March 1909 *Albatross* stn 5409.

Between Bohol and Cebu (Bohol Strait): Holotype. 1♂, USNM, 274 m, 15 March 1909, *Albatross* stn 5416. 4♂ 3♀, USNM, 265 m, 23 March 1909, *Albatross* stn 5411. 3♂ 9♀, USNM, 296 m, 23 March 1909, *Albatross* stn 5412. 2♀, USNM, 291 m, 25 March 1909, *Albatross* stn 5418. 3♀, USNM, 320 m, 25 March 1909, *Albatross* stn 5419. 1♂ 15♀, USNM, 318 m, 9 April 1908, *Albatross* stn 5197.

Mindanao: 1♂ 1♀, USNM, off Tagolo Pt, 401 m, 20 August 1909, *Albatross* tn 5541. 3♂ 8♀, USNM, off Tagolo Pt, 366 m, 9 August 1909, *Albatross* stn 5518. 1♂ 1♀, USNM, off Tagolo Pt, 320 m, 9 August 1909, *Albatross* stn 5516. 4♂ 5♀, USNM, NE Tagolo Pt, 320 m, 9 August 1909, *Albatross* stn 5517. 1♂ 2♀, USNM, E of Illana Bay, 289 m, 22 May 1908, *Albatross* stn 5256. 5♀, USNM, Gulf of Davao, 247 m, 18 May 1908, *Albatross* stn 5247.

INDONESIA—2♂ 8♀, BMNH, off Sarawak, Borneo, 198 m, 8 December 1955, *Manihini* stn C5-19. 2♂ (1♀ tentatively assigned), VNIRO. SE Timor I, Timor Sea, 320-355 m, 5 May 1963, *Lira*, O. A. Petrov.

Diagnosis.—Rostrum usually straight, sometimes slightly arched or sinuous, and long, reaching or overreaching third antennular article. Anteroventral extremity of carapace forming angle of about 90°; hepatic spine located ventral to level of antennal spine; branchiocardiac carina with anterior end relatively far from hepatic sulcus. Telson with three pairs of movable spines. Petasma with proximal plate of dorsomedian lobule bearing mesial crest; proximal process of rib of dorsolateral lobule subcircular; ventral costa ending distally in short, relatively narrow process. Thelycal plate of sternite XIV with anterior border transverse or slightly inclined posterolaterally, straight or somewhat sinuous and with anterolateral corners almost forming right angles; median ridge broadest and most salient posteriorly, usually flasklike or gently tapering anteriorly; median plate of sternite XIII cordiform, with acute apex.

Description.—Rostrum (Figure 20) almost horizontal, usually straight, sometimes slightly arched or sinuous in adult (straight or barely arcuate in young), falling short of or overreaching distal margin of antennular peduncle, its length ranging from about 0.7 to 0.8 that of carapace. Rostral plus epigastric teeth 11-18 (usually 11-14), second rostral tooth (occasionally third) located in line with orbital margin, basal teeth close together, those toward apex variously spaced, and extending almost to end of rostrum but occasionally only to base of distal 0.25. Postrostral carina low, although well defined, behind epigastric tooth, ending just behind dorsal extremity of cervical sulcus; minute dorsal tubercle located near posterior margin of carapace. Antennal spine relatively small; hepatic spine slightly larger than, and situated ventral to level of, antennal spine. Anteroventral extremity of carapace forming angle of about 90° (Figure 21*B*). Antennal carina almost indistinct; cervical carina sharp, accompanying sulcus well marked; hepatic carina broadly sigmoid, descending obliquely anteroventrally from below hepatic spine, then turning almost anteriorly in slightly concave line to apex of pterygostomian spine; branchiocardiac carina well marked, with anterior extremity not nearly reaching posterior end of hepatic sulcus and ex-

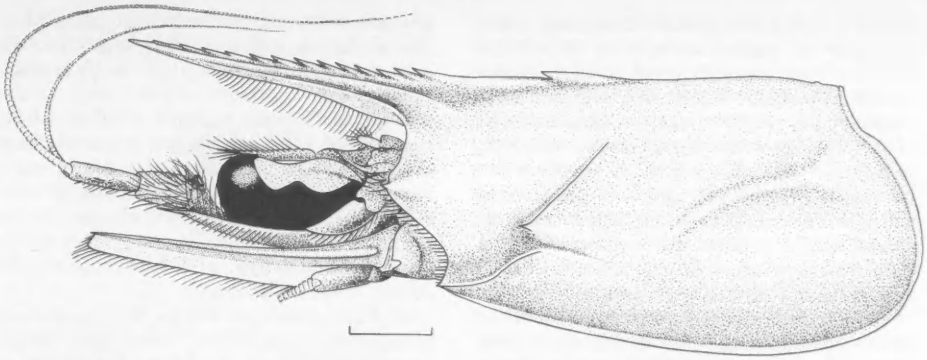

FIGURE 20.—*Penaeopsis rectacuta*, ♀ 27 mm cl, Albay Gulf, Luzon, Philippines. Cephalothorax, lateral view. Scale = 5 mm.

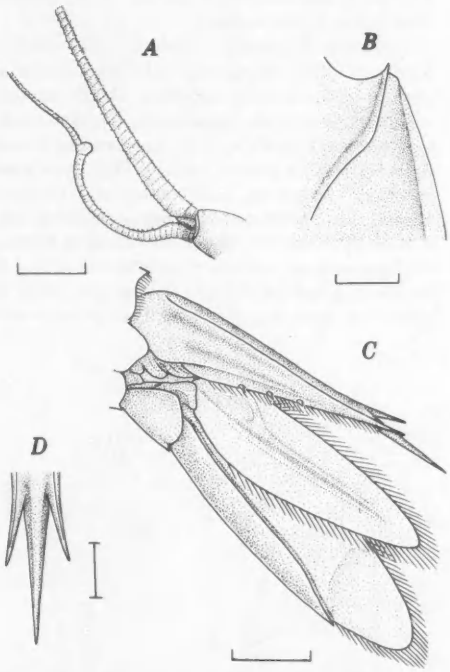

FIGURE 21.—*Penaeopsis rectacuta*. *A*, ♂ 25 mm cl, Balayan Bay, Luzon, Philippines, right flagella (mesial view). *B*, ♀ 27 mm cl, Albay Gulf, Luzon, Philippines, anteroventral part of carapace. *C*, ♀ 28.5 mm cl, Gulf of Davao, Mindanao, telson and left uropod, lateral view. *D*, Same specimen, tip of telson, dorsal view. Scales: *A*, *B*, *D* = 2 mm; *C* = 5 mm.

tending posterodorsally to rather near margin of carapace.

Antennular peduncle with length equivalent to about 0.75 that of carapace, third article slightly stouter and longer in male than in female, about 1.65 times as long as second in former and 1.40 times in latter; prosartema almost attaining distal margin of first article; distolateral spine slender, sharp, and reaching between proximal 0.3 and, at least, midlength of second article; stylocerite ending in small spine, length about 0.4 that of first article. In both sexes dorsal flagellum not evenly tapering, its stout proximal part suddenly narrowing into filiform distal part; but in male, dorsal flagellum longer than ventral, its length about 1.7 that of carapace, whereas in female, dorsal flagellum shorter than ventral, about as long as carapace. Ventral flagellum in male (Figure 21*A*) with strong knob at junction between semicircular proximal part and straight distal part; in female, ventral flagellum straight, tapering to filiform distal part. (Shape of both flagella in male and female characteristic of all species of genus.)

Scaphocerite falling short of to surpassing distal end of antennular peduncle, reaching at most as far as base of distal fourth of thickening of dorsal flagellum; lateral rib ending in slender spine, not quite reaching distal margin of lamella. Antennal flagellum broken in shrimp examined.

Third maxilliped extending at least to basal 0.2 of second antennular article and at most to midlength of third; ratio of dactyl/propodus about 0.65 in males and 0.70 in females.

First pereopod exceeding carpocerite by tip of dactyl or by as much as length of propodus. Second pereopod surpassing carpocerite at least by length of propodus and at most by propodus and 0.3 length of carpus (i.e., reaching between base of

second article and proximal 0.2 of third). Third pereopod of male overreaching antennular peduncle by as much as length of dactyl, that of female, by propodus. Fourth pereopod surpassing carpocerite by length of dactyl or by a maximum of dactyl and propodus. Fifth pereopod exceeding antennular peduncle by dactyl or by latter plus 0.4 length of propodus. Order of pereopods in terms of their maximum extensions: first, fourth, second, fifth, and third; fourth pereopod extending almost as far as second, and fifth almost as far as (occasionally farther than) third.

Abdomen with sixth somite elongate, about 1.7 times maximum height, bearing rather prominent interrupted cicatrix on lateral surface. Telson (Figure 21*C*) with lateral margins bearing three pairs of short movable spines; fixed spines moderately long, extending at most as far as base of distal third of terminal portion; terminal portion (Figure 21*D*) with length 6-8 times basal width, flasklike in shape, its lateral margins convex or forming widely obtuse angles anteriorly, converging posteriorly, and with dorsal surface subplane. Mesial ramus of uropod reaching apex of telson or overreaching it by as much as 0.20 of its own length; lateral ramus overreaching mesial by about 0.25 of its own length.

Petasma (Figure 22*A*, *B*) with dorsomedian lobule produced into rather broad distomedian projection, and bearing elongate distal plate and broader, subtriangular proximal plate raised mesially in low, sometimes sharp crest; rib of dorsolateral lobule terminating proximally in subcircular process. Ventrolateral lobule with distolateral portion broadly rounded, bearing distally rather flexible and translucent marginal region, strongly reflexed inwardly; distal part of ventral costa curving abruptly dorsomesially at about right angle, and ending in short, relatively narrow process (free from, though closely appressed to, margin of dorsolateral lobule) reaching approximately to level of cincinnuli.

Appendix masculina (Figure 22*C*) considerably broader than long (width 1.7-2.0 length), roughly kidney-shaped; band of relatively long setae extending around free margin, broadening and forming patch mesially, or setae covering more than half of dorsal surface.

Thelycum (Figures 23; 24*A*, *B*) with anterior border of plate of sternite XIV transverse or slightly inclined posterolaterally, almost straight or somewhat sinuous on each side of posteromedian projection of sternite XIII, and forming almost right angle with lateral borders. Plate (produced anteriorly in paired small submesial lobules), densely setose laterally, strongly slanting dorsomesially toward deep, usually narrow, submedian depressions; median ridge of variable length, broadening and much higher posteriorly, usually appearing flask-shaped, its bulbous portion cov-

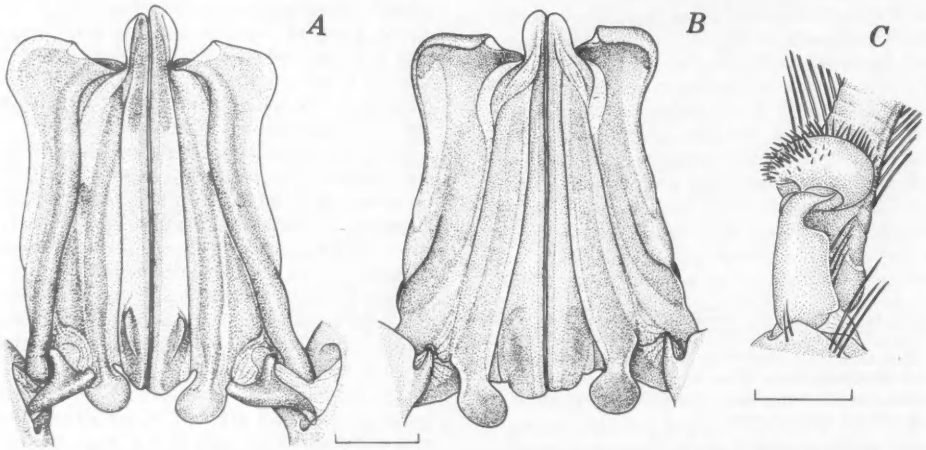

FIGURE 22.—*Penaeopsis rectacuta*, ♂ 17.5 mm cl, Singapore. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scale = 1 mm.

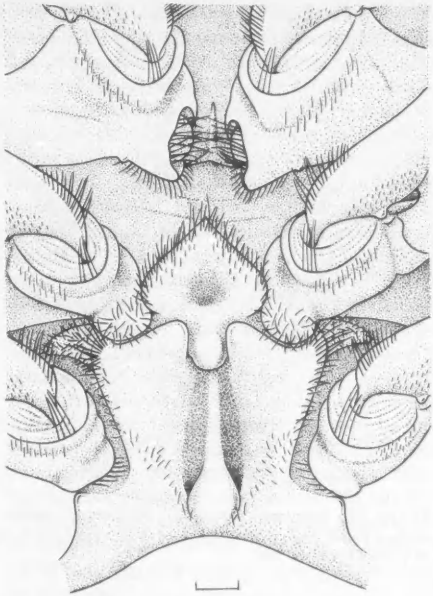

FIGURE 23.—*Penaeopsis rectacuta*, holotype ♀ 24 mm cl, Bohol Strait, Philippines. Thelycum, ventral view. Scale = 1 mm.

ered with setae. Posterior thoracic ridge fringed anteriorly with closely set setae. Median plate of sternite XIII cordiform (with acute apex), covered with setae except for central depression (occasionally prolonged across entire width of plate); posteromedian projection subrectangular or subelliptical, with posterior margin entire or, occasionally, shallowly emarginate. Sternite XII bearing posteromedian, often laterally compressed tooth of variable size, sometimes produced in apical spine; oblique pair of sharp ridges extending posterolaterally from base of tooth.

Thelycum in young females (9-11 mm cl) with median plate of sternite XIII produced anteriorly in long, slender spine, and posteromedian projection consisting of only minute knob; plate of sternite XIV bearing short median ridge also produced anteriorly in long, slender spine, latter indistinct in females 13 mm cl.

The female holotype, 26 mm cl, is in poor condition, with many parts missing; however, except for the rostrum, which is almost entirely lost, the carapace is well preserved as are the antennular peduncle, most of the abdomen, and the thelycum. The following characters of the carapace may be readily observed: the second rostral tooth is situated opposite the orbital margin, while the

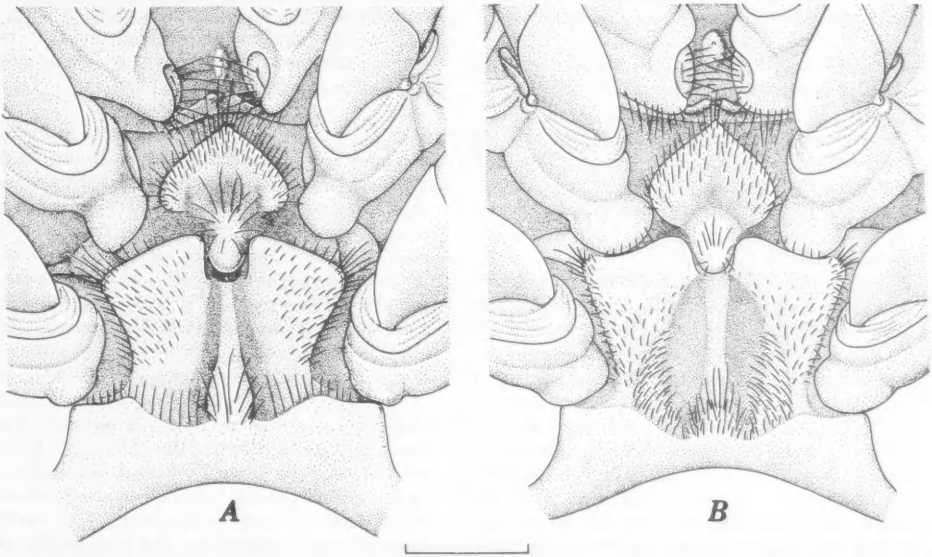

FIGURE 24.—*Penaeopsis rectacuta*. *A*, ♀ 25.5 mm cl, off Tagolo Point, Mindanao, Philippines. *B*, ♀ 24 mm cl, Tabayas Bay vicinity of Marinduque Island, Philippines. Thelyca, ventral view (setae omitted on the legs). Scale = 2 mm.

epigastric tooth is found at the anterior 0.35 of the carapace, and the hepatic spine lies conspicuously ventral to the antennal spine; the postrostral carina extends along anterior 0.55 of the carapace, ending just posterior to the cervical sulcus; and the anteroventral corner forms an angle of about 90°. The antennular peduncle is 0.75 as long as the carapace, the third article is 1.35 times the length of the second, and the stylocerite is 0.4 that of the first article. The scaphocerite falls slightly short of the end of the antennular peduncle, and the terminal spine of the lateral rib does not reach the distal margin of the lamella. The low, sharp middorsal keel of the abdomen extends from the fourth to the sixth somites, and the length of the latter is 1.7 times its maximum height. The thelycum is depicted in Figure 23.

In this species each spermatophore bears a conspicuous, somewhat rigid element which in impregnated females lies over the plate of sternite XIV (Figure 25). The paired elements, which project from the mesial extremity of the sperm sacs enclosed in the seminal receptacles, are joined along their mesial margins and form a roughly circular scale covering a large part of the plate. A similar spermatophore is also found in *P. balssi*, *P. eduardoi*, and *P. jerryi*, the other three Indo-West Pacific species in which I have observed impregnated females.

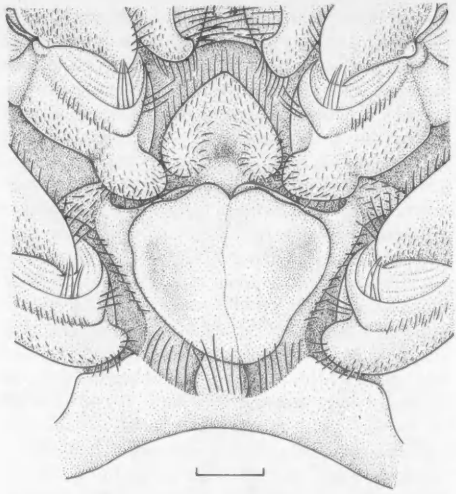

FIGURE 25.—*Penaeopsis rectacuta*, ♀ 25.5 mm cl, vicinity of western Bohol, Philippines. Compound spermatophore attached to female. Scale = 1 mm.

Maximum lengths.—Males 25 mm cl, about 110 mm tl; females 31 mm cl, about 135 mm tl.

Geographic and bathymetric ranges.—Indo-West Pacific (Figure 6) from the Philippines (Bate 1881) and Timor Sea to the south China Sea (north of Borneo, Hall 1962). It has been found at depths between 174 and 401 m.

Affinities.—Two features of the carapace distinguish *P. rectacuta* from the closely allied, western Indo-West Pacific *P. jerryi*: 1) the position of the hepatic spine, which in the former is situated distinctly ventral to the antennal spine whereas it occurs at about the same level in *P. jerryi*, and 2) the length of the branchiocardiac carina which is relatively short in *P. rectacuta* (its anterior extremity situated well behind the posterior end of the hepatic sulcus) and is long in *P. jerryi* (its anterior extremity located quite near the posterior end of the sulcus). In addition, the thelycum of *P. rectacuta* has the anterior border of the plate of sternite XIV almost straight or slightly sinuous and forms an angle with the lateral border, whereas in *P. jerryi* it is strongly convex and continuous through a broad arc with the lateral border. Furthermore, the median plate of sternite XIII is cordiform and rather elongate in *P. rectacuta* and subsemicircular, or occasionally trilobed in *P. jerryi*.

Variation.—This shrimp exhibits a rather large number of morphological variations. In the adult the rostrum may be straight, slightly convex or sinuous, and the number of rostral teeth ranges from 10 to 17. The scaphocerite falls short of, reaches as far as or extends beyond, the antennular peduncle. In the females, the anterior border of the plate of sternite XIV (Figure 24*A*, *B*) varies from transverse to slightly inclined posterolaterally, the median ridge may be short or extend to the posteromedian projection of sternite XIII, and the submedian depressions that flank the ridge, although most often narrow, may be broad. Furthermore, the setation of the plate, usually extending over the lateral portions, sometimes is absent anteriorly and lacking posteriorly or vice versa. The median plate of sternite XIII usually bears a central depression, but occasionally the latter extends across the entire width of the plate, and the caudal margin of the posteromedian pro-

jection, which is straight in most specimens, sometimes exhibits a shallow emargination. Finally, the tooth on sternite XII may vary considerably in size and shape; although usually compressed, it may be subconical or infrequently strongly produced in an apical spine. Sometimes the entire range of variation of certain characters is represented within a single lot. Among the 16 specimens collected at *Albatross* stn 5197, off western Bohol, Philippines, the number of rostral teeth ranges from 11 to 17 and in several lots females, in which the posteromedian projection of sternite XIII is straight caudally were found together with others bearing a slightly emarginate one. These variations, thus, are intraspecific, not even associated with local populations.

A discussion of the features that separate this species from *P. eduardoi* was presented by Pérez Farfante (1977b). As noted by Hall (1962), typical *P. rectacuta* possesses longer pereopods than do specimens reported by De Man (1911) as "*Parapenaeus rectacutus*," which actually are *Penaeopsis eduardoi*. In *P. rectacuta*, however, the third maxilliped is slightly shorter than that of *P. eduardoi*.

Remarks.—The specimens from off Borneo recorded by Hall (1962) as *P. rectacuta* were in my opinion, correctly identified. The suggestion by Ivanov and Hassan (1976) that they might belong to *P. balssi*—under the synonymy of which the authors, "with some hesitation," included the record preceded by a question mark—is not justified. I have found that the petasmata of these specimens are typical and the thelyca vary but slightly from that of the holotype. The only obvious difference is that in the females, the median ridge of the plate of sternite XIV, although broadest posteriorly, is not flasklike. Also, this plate is rather densely setose laterally, as indicated by Ivanov and Hassan, and the transverse thoracic ridge bears a row of setae across the anterior border which is lacking in the holotype; it is probable that in the latter the setae have been lost, as have almost the entire rostrum, telson, and at least part of the appendages during or after capture.

Pérez Farfante (1978) described three specimens found in the waters of the Philippines having gonopores on the coxae of the fifth pair of pereopods and both male and female genitalia. The petasma, appendix masculina, and thelycum of the three exhibit unique features, but in most respects these shrimp are markedly similar to members of *P. rectacuta*. It was concluded that they are probably anomalus intersexes of this species. Recently, Boris G. Ivanov of VNIRO, kindly made available to me three specimens (two males and one female; Figures 26*A-C*; 27)

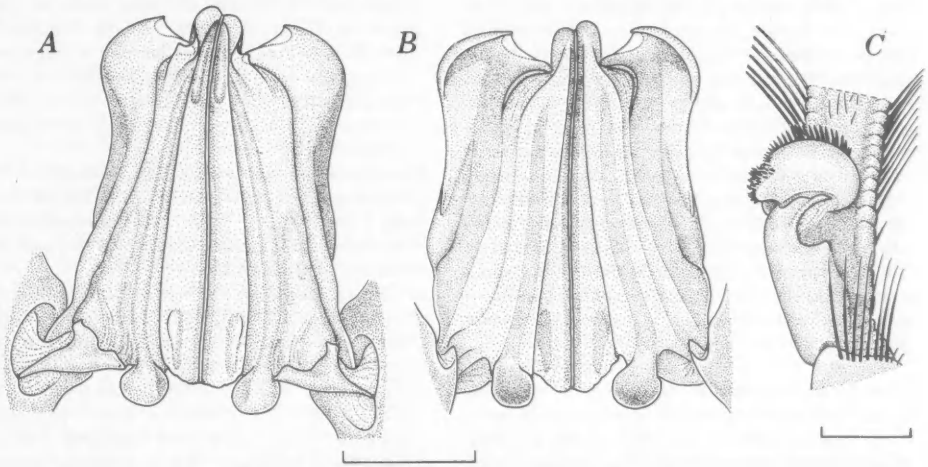

FIGURE 26.—*Penaeopsis rectacuta*, ♂ 21 mm cl, S of Timor Island, Timor Sea. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. Scales: *A*, *B* = 2 mm; *C* = 1 mm.

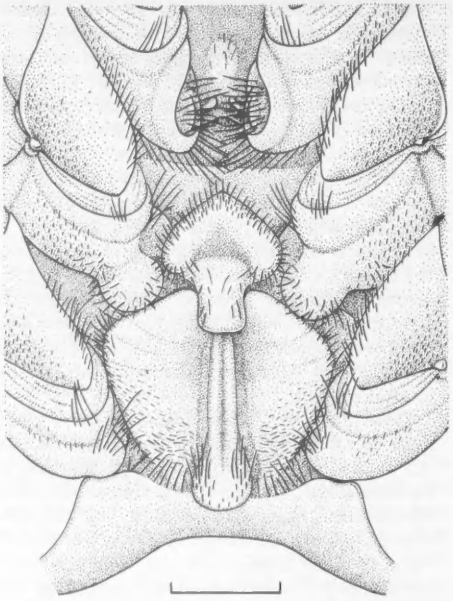

FIGURE 27.—*?Penaeopsis rectacuta*, ♀ 31 mm cl, S of Timor Island, Timor Sea. Thelycum, ventral view. Scale = 2 mm.

collected in the Timor Sea by O. A. Petrov during a cruise of the RV *Lira*. There is little doubt in my mind that the males are members of *P. rectacuta*. The female, except for the thelycum, also possesses features typical of *P. rectacuta*. In the thelycum the anterior border of the plate of sternite XIV is considerably more inclined posterolaterally than in typical females. The anterior part of the median ridge is uniquely divided by a groove, and the bulbous posterior part is larger and overlaps the thoracic ridge. Finally, the posteromedian projection of sternite XIII is considerably larger than in any specimen of *P. rectacuta* examined by me. A bopyrid isopod was found in the branchial chamber of this specimen; it might have been responsible for these peculiar features of the female genitalia.

Commercial importance.—Although no estimates of the economic importance of this species have been recorded, it has been cited among the commercially exploited shrimps of the Philippines by Domantay (1956), and as of economic value throughout its range by Holthuis and Rosa (1965).

Penaeopsis serrata Bate 1881

Figures 28-38

Penaeopsis serratus Bate 1881:183 [syntypes by implication, 1♂ 1♀, MCZ 7200, 1♀, MP; type-locality, off Barbados, "Gulf of Mexico," *Blake* stn 275, 218 fathoms (399 m)]. Bouvier 1905a:981; 1908:5. A. Milne Edwards and Bouvier 1909:221, pl. 4, fig. 1-4. De Man 1911:53. Balss 1925:229. Schmitt 1926:320. Boone 1927:80 [part]. Maurin 1952:91; 1961:530; 1962:210; 1963:1. Burkenroad 1963:172. Maurin 1965:116; 1968a:33; 1968b:479, fig. 3 *P. s.* Lagardère 1971:33, fig. 39-42. [Placed on the Official List of Specific Names in Zoology as Name No. 2276, International Commission on Zoological Nomenclature 1969, Opinion 864:141].

Parapenaeus megalops Smith 1885:172 [syntypes, 2♀, USNM 7262, S of Curaçao, 11°43′ N, 69°09′30″ W, 208 fathoms (380 m), *Albatross* stn 2125. 5♂ 1♀, USNM 7263, Golfo de Urabá, 9°30′45″ N, 76°25′30″ W, 155 fathoms (283 m), *Albatross* stn 2143]. Rathbun 1901:102. Bouvier 1908:7. A. Milne Edwards and Bouvier 1909:225. Hay and Shore 1918:379, pl. 25, fig. 8. Schmitt 1926:319.

Parapeneus megalops. Faxon 1896:163. Alcock 1905:520; 1906:52.

Artemesia talismani Bouvier 1905a:982 [syntypes, 2♂ 2♀, MP 304, off Guerguerat, Western Sahara, 25°41′ N, 15°56′ W (of Greenwich; 18°16′ W of Paris on label accompanying specimens), 410 m, 9 July 1883, *Talisman* stn 72; type-locality, "côtes du Maroc et du Sahara"]; 1908:7. A. Milne Edwards and Bouvier 1909:225.

Penaeopsis serratus var. *antillensis* A. Milne Edwards and Bouvier 1909:226, pl. 3, fig. 10, pl. 4, fig. 5 [holotype, ♂, MCZ 7201; type-locality, off St. Kitts, 208 fathoms (380 m) 1978-79, *Blake* stn 148]. De Man 1911:53.

Penaeopsis megalops. De Man 1911:53. Schmitt 1926:320. Burkenroad 1936:139. Kubo 1949:321. Voss 1955:8, fig. 19. Burkenroad 1963:172. Bullis and Thompson 1965:5. Joyce and Eldred 1966:26. Anderson and Bullis 1970:116. Roberts and Pequegnat 1970:49. Pequegnat and Roberts 1971:8. Longhurst 1971:237. Pérez Farfante 1971:4. Crosnier and Forest 1973:305. Burukovsky 1974:31.

Parapeneus paradoxus. Boone 1927:79 [part; not *Neopenaeopsis paradoxus* Bouvier 1905b = *Peneus longirostris* Lucas 1846].

Penaeopsis (Penaeopsis) megalops. Burkenroad 1934a:12, fig. 1. Anderson and Lindner 1945:309. Springer and Bullis 1956:9.

Peneopsis megalops. Bullis 1956:10. Bullis and Rathjen 1959:18.

Penaeopsis serrata. Holthuis and Rosa 1965:4. Longhurst 1971:220. Ivanov and Hassan 1976:4. Pérez Farfante 1977a:297; 1977b:180. Pérez Farfante and Ivanov 1979:204. Pérez Farfante 1979:208. Wenner and Boesch 1979:110.

Common names: megalops shrimp; camarón megalops; crevette megalops.

Material.

UNITED STATES—New Jersey: 1♀, USNM, E of Barnegat, 275-290 m, 12 August 1972, *Gosnold* cruise 197, stn 111.

North Carolina: 3♀, USNM, off Back Bay, 331 m, 23 July 1969, *Oregon II* stn 10659. 11♂ 8♀, USNM, SE of Cape Lookout, 366 m, 10 June 1962, *Silver Bay* stn 4160. 11♂ 7♀, USNM, off Carolina Beach, 412 m, 16 November 1956, *Combat* stn 178. 27♂ 37♀, USNM, SE of Cape Fear, 459 m, 16 November 1956, *Combat* stn 179.

South Carolina: 2♂ 8♀, USNM, off Charleston, 366 m, 28 May 1949, *Albatross III* stn 1922. 1♂ 1♀, USNM, off Port Royal Sound, 366 m, 23 January 1972, *Oregon II* stn 11734.

Georgia: 1♀, USNM, off Ossawa, 183 m, 21 January 1972, *Oregon II* stn 11719. 1♂ 1♀, USNM, off Ossawa, 238 m, 21 January 1972, *Oregon II* stn 11720.

Florida: 2♂ 6♀, USNM, off St Augustine, 329 m, 20 January 1972, *Silver Bay* stn 3677. 2♀, USNM, off Flagler Beach, 338 m, 3 February 1962, *Silver Bay* stn 3728. 2♂ 2♀, UMML, off Delray Beach, 549 m, 13 September 1966, *Gerda* stn 806. 1♂ 3♀, FIU, NW of Cayo Sal Bank, 366 m, 14 May 1978, *Bellow* stn 5 #3. 10♂ 8♀, USNM, SW of Marquesas Keys 402-269 m, 2 February 1968, *Gerda* stn 969. 6♂ 7♀, USNM, S of Dry Tortugas, 366 m, 10 July 1955, *Oregon* stn 1330. 15♂ 21♀, UMML, S of Dry Tortugas, 329-366 m, 28 April 1969, *Gerda* stn 1096. 30♂ 28♀, USNM, S of Dry Tortugas, 348 m, 13 April 1954, *Oregon* stn 1005. 7♂ 38♀, USNM, 31 July 1930, stn 37-38; 3♂ 20♀, USNM, 402-433 m, 31 July 1930, stn 38-30; 8♂ 13♀, USNM, 366-430 m, 8 July 1931, stn 21-31; 28♂ 113♀, USNM, 256-329 m, 31 July 1931, stn 37-30; 2♂, USNM, 256-360 m, 30 July 1932, stn 67-32; all from the Tortugas area, W. L. Schmitt. 9♂ 15♀, USNM, NW of Dry Tortugas, 366 m, 10 June 1959, *Silver Bay* stn 1201. 7♂ 2♀, USNM, S of St George I, 366 m, 21 August 1970, *Oregon II* stn 11180. 15♀, USNM, S of Gulf Beach, 274 m, 16 June 1964, *Oregon* stn 4946.

Alabama: 9♂ 21♀, USNM, off Mobile Bay, 320 m, 27 April 1951, *Oregon* stn 314.

Louisana (all from Mississippi Delta area): 14♂ 55♀, USNM, 274 m, 23 October 1962, *Oregon* stn 4002. 9♂ 15♀, USNM, 732 m, 3 June 1959, *Silver Bay* stn 1181. 1♂ 3♀, USNM, 366 m, 31 January 1955, *Oregon* stn 1238.

Texas: 10♀, USNM, off Galveston, 476 m, 13 March 1969, *Oregon II* stn 10616. 3♂ 16♀, USNM, off Galveston, 457-549 m, 16 April 1952, *Oregon* stn 542. 32♂ 38♀, USNM, off Padre I, 366 m, 28 November 1950, *Oregon* stn 162. 3♂ 8♀, USNM, off Padre I, 430 m, 28 November 1950, *Oregon* stn 163. 1♀, USNM, off Port Isabel, 457-476 m, 5 August 1969, *Western Gulf* stn 37.

MEXICO (GULF OF MEXICO)—Tamaulipas: 1♂ 1♀, USNM, off Los Lavaderos, 558 m, 2 June 1970, *Oregon II* stn 10953. 3♂ 2♀, USNM, SW of Soto la Marina, 329 m, 1 June 1970, *Oregon II* stn 10951.

Veracruz: 2♀, USNM, off Tecolutla, 375 m, 4 June 1970, *Oregon II* stn 10958. 2♀, USNM, NE of Punta Roca Partida, 613 m, 5 June 1970, *Oregon II* stn 10960.

Tabasco: 1♀, USNM, W of Laguna del Carmen, 430 m, 6 June 1970, *Oregon II* stn 10963.

Campeche: 1♀, USNM, off Punta Frontera, 366 m, 15 May 1954, *Oregon* stn 1054.

Yucatan; 46♂ 78♀, USNM, Yucatan Channel, 377 m, 19 June 1952, *Oregon* stn 590.

BAHAMA ISLANDS—1♀, USNM, NW of Matanilla Reef, 567 m, 17 July 1965, *Gerda* stn 664. 2♂ 6♀, USNM, W of Grand Bahama I, 494-531 m, 13 June 1969, *Gerda* stn 1125. 9♂ 3♀, USNM, Santaren Channel, 508 m, 22 June 1967, *Gerda* stn 817.

CUBA—30♂ 36♀, USNM, NE of Las Villas 516 m, 27 June 1970, *Pillsbury* stn 1171. 67♂ 24♀, USNM, off Las Villas, 512 m, 16 July 1955, *Oregon* stn 1342. 34♂ 37♀, USNM, off Archipiélago de Sabana, 466 m, 16 December 1969, *Oregon II* stn 10863. 2♂ 7♀, MCZ, Bahía de Cochinos, 274-311 m, 25 February 1938, *Atlantis* stn 2963B. 3♂ 2♀, MCZ, Bahía de Cochinos, 402-

503 m, 25 February 1938, *Atlantis* stn 2963D.

JAMAICA—6♂ 4♀, USNM, off Great Pedro Bluff, 530 m, 16 May 1962, *Oregon* stn 3552. 1♂ 3♀, USNM, off Great Pedro Bluff, 311 m, 16 May 1962, *Oregon* stn 3549.

DOMINICAN REPUBLIC—10♂ 5♀, USNM, off Puerto Plata, 421-549 m, 15 October 1963, *Silver Bay* stn 5166. 2♀, USNM, off El Macao, 549 m, 17 October 1963, *Silver Bay* stn 5181.

VIRGIN ISLANDS—2♂ 2♀, USNM, N of Virgin Is, 165-915 m, 4 March 1933, Johnson-Smithsonian Deep Sea Expedition stn 102. 1♀, USNM, off Charlotte Amalie, 402 m, 26 September 1959, *Oregon* stn 2606.

PUERTO RICO—1♀, USNM, N of Culebra I, 366-732 m, 26 February 1933, Johnson-Smithsonian Deep Sea Expedition stn 81. 2♂ 6♀, USNM, off San Juan, 256-293 m, 25 September 1959, *Oregon* stn 2603. 4♂, USNM, NE of Puerto Rico, 183-549 m, 4 March 1933, Johnson-Smithsonian Deep Sea Expedition stn 100. 2♂ 2♀, USNM, off Añasco, 549 m, 6 October 1959, *Oregon* stn 2652.

LESSER ANTILLES—7♀, USNM, NW of Dog I, 628 m, 6 December 1969, *Oregon II* stn 10835. 1♀, USNM, W of Anguilla, 658 m, 7 December 1969, *Oregon II* stn 10837. 29♂ 14♀, USNM, E of Saba, 549-585 m, 18 May 1967, *Oregon* stn 6695. 13♂ 17♀, USNM, E of St Christopher, 578 m, 8 December 1969, *Oregon II* stn 10842. 13♂ 9♀, UMML, E of Capesterre, Guadeloupe, 466-640 m, 16 July 1969, *Pillsbury* stn 936. 25♂ 17♀, USNM, off Dominica, 503 m, 4 March 1966, *Oregon* stn 5926. 13♂ 14♀, USNM, E of Dominica, 649 m, 5 March 1966, *Oregon* stn 5929. 2♂ 4♀, UMML, SE of Pointe du Cap, St Lucia, 274-567 m, 7 July 1969, *Pillsbury* stn 891. 3♂ 2♀, USNM, E of Georgetown, St Vincent, 348-466 m, 6 July 1969, *Pillsbury* stn 877. 1♂ 1♀, MCZ 7200, + 1♀, MP, syntypes of *Penaeopsis serratus* Bate, off Barbados, 399 m, 5 March 1879, *Blake* stn 275. 11♂ 5♀, USNM, S of Bonaire, 393 m, 27 September 1963, *Oregon* stn 4405. 1♀, USNM, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125. 2♀, syntypes of *Parapenaeus megalops* Smith, USNM 7262, S of Curaçao, 380 m, 18 February 1884, *Albatross* stn 2125.

WESTERN CARIBBEAN—20♂ 16♀, USNM, Arrowsmith Bank, 225-250 m, 14 March 1958, *Pillsbury* stn 587. 18♂ 5♀, USNM, NW of Rosalind Bank, 274 m, 7 June 1962, *Oregon* stn 3628. 23♀, USNM, NW of Rosalind Bank, 366 m, 23 August 1957, *Oregon* stn 1883. 8♂ 83♀, USNM, W of Quita Sueño Bank, 450-576 m, 31 January 1971, *Pillsbury* stn 1355. 1♂ 5♀, USNM, W of I de Providencia, 457 m, 21 November 1968, *Oregon II* stn 10200. 7♂ 4♀, USNM, W of I de San Andrés, 457 m, 23 May 1962, *Oregon* stn 3572.

MEXICO (CARIBBEAN SEA)—Quintana Roo: 1♀, RMNH, SE of I Mujeres, 567-570 m, 23 May 1967, *Pillsbury* stn 585. 1♂, USNM, W of I de Cozumel, 439-463 m, 16 March 1968, *Pillsbury* stn 600. 26♂ 34♀, USNM, W of I de Cozumel, 412-457 m, 16 March 1968, *Pillsbury* stn 602.

BRITISH HONDURAS—92♀, USNM, NE of Stann Creek, 219-311 m, 10 June 1962, *Oregon* stn 3637. 25♂ 11♀, YPM, N of Glover Reef, 669 m, 20 April 1925, *Pawnee* stn 35. 9♂ 32♀, YPM, N of Glover Reef, 885 m, 20 April 1925, *Pawnee* stn 36.

NICARAGUA—2♀, USNM, NE of Is del Maíz, 549-585, 23 May 1962, *Oregon* stn 3576.

PANAMA—1♀, USNM, off Bocas del Toro, 512 m, 25 May 1962, *Oregon* stn 3583. 1♂ 2♀, USNM, Golfo de los Mosquitos, 457 m, 31 May 1962, *Oregon* stn 3599. 3♀, USNM, NE of Belén, 439 m, 30 May 1962, *Oregon* stn 3592.

COLOMBIA—5♂ 1♀, syntypes of *Parapenaeus megalops* Smith 1885, USNM 7263, Golfo de Urabá, 283 m, 23 March 1884, *Albatross* stn 2143. 1♀, UMML, SW of I de Barú, 135-130 m, 14 July 1966, *Pillsbury* stn 375. 19♀, USNM, off I de Barú, 366 m, 25 May 1964, *Oregon* stn 4882. 12♀, USNM, W of Cartagena, 170-150 m, 1 August 1968, *Pillsbury* stn 797. 1♀, USNM, off Cabo de la Aguja, 176-165 m, 31 July 1968, *Pillsbury* stn 785. 3♂ 2♀, USNM, W of Cabo de la Vela, 357 m, 20 November 1970, *Oregon II* stn 11289.

VENEZUELA—7♂ 7♀, UMML, NE of San Juan de los Cayos, 384-607 m, 26 July 1968, *Pillsbury* stn 753. 23♂ 6♀, USNM, off Is Los Testigos, 366-439 m, 24 September 1964, *Oregon* stn 5037. 5♂ 2♀, USNM, NE of Punta Araguapiche, 366 m, 3 November 1957, *Oregon* stn 1981.

TRINIDAD-TOBAGO—1♀, USNM, NE of Charlotteville, 165-183 m, 21 September 1964, *Oregon* stn 5021.

GUYANA—3♂ 3♀, USNM, NE of Berbice R, 366 m, 6 November 1957, *Oregon* stn 2004.

FRENCH GUIANA—1♂ 14♀, USNM, N of Roche Brigandin, 457 m, 10 November 1957, *Oregon* stn 2028.

BRASIL—2♂ 2♀, USNM, SE of Rio Grande do Sul, 345-260 m, 19 January 1967, *Akademic Knipovich*.

MOROCCO—2♀, RMNH, off Rabat, 300-600 m, 12 May 1971, Cadiz trawlers, RMNH Expedition. 2♀, RMNH, Casablanca, 28 June 1951, C. Maurin.

WESTERN SAHARA—1♂ 3, VNIRO-USNM, N of Boca Grande, 640-600 m, 11 May 1965, R. N. Burukovsky. 1♂ 3♀, VNIRO-USNM, off Villa Bens, 420-380 m, 11 May 1965, R. N. Burukovsky. 2♂ 2♀, MP 304, syntypes of *Artemesia talismani* Bouvier 1905, off Guerguerat, 410 m, 9 July 1883, *Talisman* stn 72.

Diagnosis.—Rostrum straight, basally arcuate or sinuous, and long, reaching or overreaching third antennular article. Anteroventral angle of carapace broadly obtuse. Telson with two (rarely three) pairs of movable spines. Petasma with proximal plate of dorsomedian lobule thickened mesially but lacking mesial crest; proximal process of rib of dorsolateral lobule subrectangular; ventral costa ending distally in relatively broad, inwardly excavate process. Thelycal plate of sternite XIV with anterior border broadly arched on each side of posteromedian projection of sternite XIII, and anterolateral extremities uniquely produced into lobules of variable lengths; median ridge usually ovoid or tear-shaped; median plate of sternite XIII subsemicircular to roughly pentagonal with depression extending across entire width.

Description.—Rostrum (Figures 28, 29) almost horizontal or somewhat upturned, variable in shape, straight, or basally arcuate or sinuous (strongly arched in young, Figure 30), and long, reaching between midlength of third article of antennular peduncle and proximal fourth of thickened portion of dorsal flagellum, its length rang-

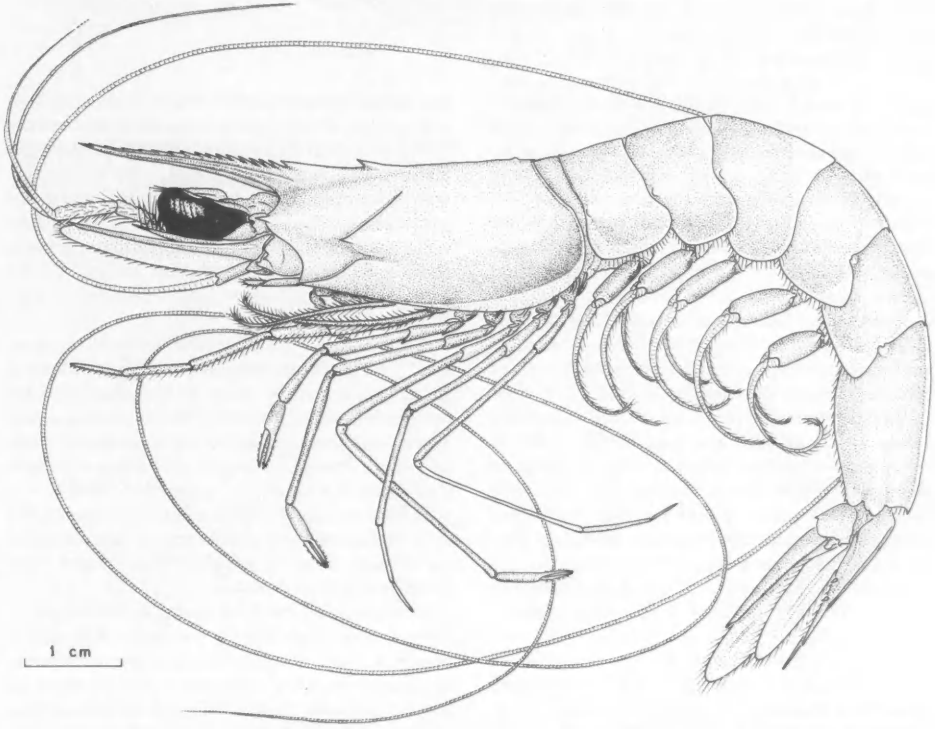

FIGURE 28.—*Penaeopsis serrata*, ♀ 27 mm cl, W of Puerto Rico. Lateral view. Scale = 10 mm.

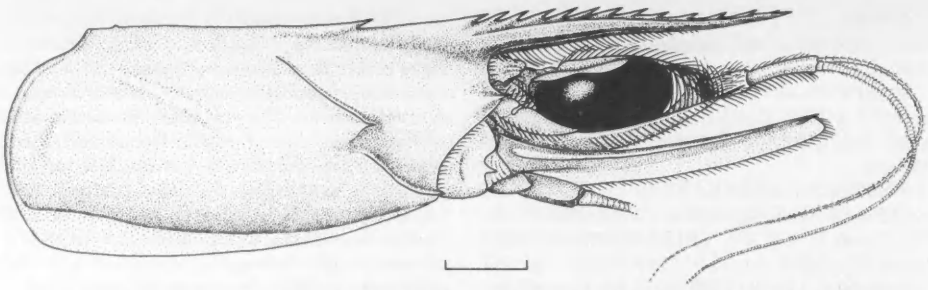

FIGURE 29.—*Penaeopsis serrata*, ♀ 27 mm cl, Golfo de los Mosquitos, Panama. Cephalothorax, lateral view. Scale = 5 mm.

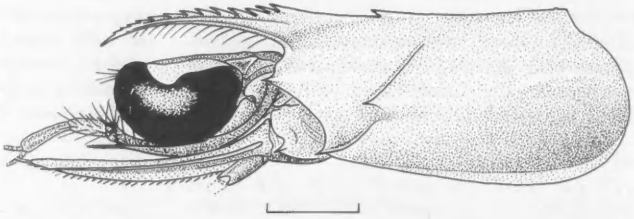

FIGURE 30.—*Penaeopsis serrata*, ♀ juvenile 9.5 mm cl, Northwest Providence Channel, Bahamas. Cephalothorax lateral view. Scale = 3 mm.

ing from about 0.65 to 0.85 that of carapace. Rostral plus epigastric teeth 10-19 (rarely <13 or >16), basal rostral teeth close together, those toward apex variously spaced; second or first (latter usually in young) rostral tooth situated in line with orbital margin. Postrostral carina low, although well defined, behind epigastric tooth ending at about level of dorsal extremity of cervical sulcus; small dorsal tubercle located near posterior margin of carapace. Antennal and hepatic spines subequal in size, latter situated distinctly ventral to antennal spine. Anteroventral angle of carapace broadly obtuse (Figure 31*A*). Antennal carina short; cervical carina sharp, accompanying sulcus well marked; hepatic carina sigmoid anteriorly (from below hepatic spine to apex of pterygostomian spine), hepatic sulcus well marked along carina, shallow posteriorly. Branchiocardiac carina very weak, extending posterodorsally to near margin of carapace.

Antennular peduncle with length equivalent to about 0.70 that of carapace, third article sexually dimorphic, slightly longer and considerably stouter in males than in females, about 1.4 times as long as second in former and 1.2 times in latter; prosartema reaching, or almost reaching, distomesial margin of eye; distolateral spine long, slender, and sharp, reaching between midlength and distal fourth of second article; stylocerite ending in small spine, about 0.4 as long as first article. In male, ventral flagellum shorter (even when forcibly straightened) than dorsal, with inconspicuous knob at junction between proximal and distal parts; dorsal flagellum 1.5-1.8 times as long as carapace. In female, ventral flagellum (tapering to filiform distal part) longer than dorsal, 1.5-1.7 times as long as carapace; dorsal flagellum 0.8-1.0 times as long.

Scaphocerite falling slightly short of to somewhat overreaching antennular peduncle; lateral rib ending in slender spine, falling short of distal margin of lamella. Antennal flagellum long, about 3 times tl of shrimp (based on measurements made by me on freshly collected specimens during a Caribbean Sea cruise of *Oregon II* in 1969).

Third maxilliped extending at least to basal 0.4 of second antennular article and at most to distal end of third; ratio of dactyl/propodus about 0.75 in males and 0.85 in females.

First pereopod reaching distal end of carpocerite or overreaching it by as much as 0.8 length of propodus. Second pereopod surpassing carpocerite by at least length of propodus and by as much as that of propodus and half length of carpus (i.e., reaching between base of second antennular article and midlength of third). Third pereopod

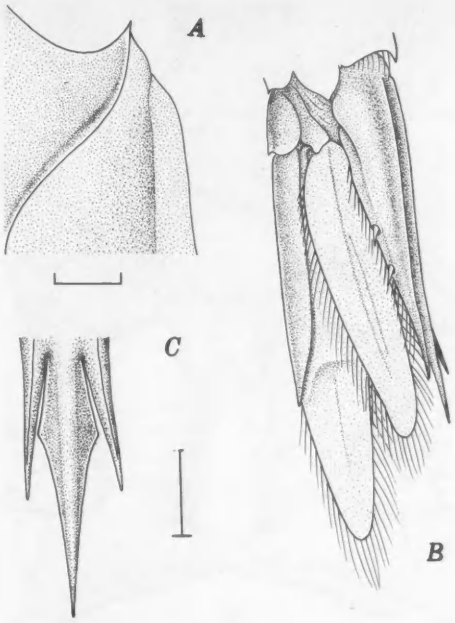

FIGURE 31.—*Penaeopsis serrata*, ♀ 29.5 mm cl, Dry Tortugas Islands, Fla. *A*, Anteroventral part of carapace. *B*, Telson and left uropod. *C*, Tip of telson. Scales: *A*, *C* = 2 mm; *B* = 5 mm.

attaining distal end of antennular peduncle or overreaching it by as much as length of propodus. Fourth pereopod surpassing carpocerite by tip of dactyl or by maximum of dactyl plus about one-half length of propodus. Fifth pereopod extending at least to midlength of second antennular article and at most to distal end of third. Order of pereopods in terms of their maximum anterior extensions: first, fourth, second, fifth, and third; fourth pereopod extending almost as far as second. Third maxilliped reaching about as far as fifth pereopod.

Abdomen with sixth somite elongate, about 1.8 times maximum height, bearing faint, interrupted cicatrix on lateral surface. Telson (Figure 31*B*) with lateral margins armed with two (rarely three) pairs of short, slender movable spines; fixed spines moderately long, extending at most as far as base of distal third of terminal portion; terminal portion (Figure 31*C*) with length 6-9 times basal width, spear shaped and with dorsal surface convex. Mesial ramus of uropod almost reaching or surpassing apex of telson by as much as 0.15 of its own length; lateral ramus overreaching mesial ramus by 0.25-0.30 of its own length.

Petasma (Figure 32*A*, *B*) with dorsomedian lobule produced in well-defined distomedian projection, bearing narrow distal plate and broader proximal plate thickened mesially, but not form-

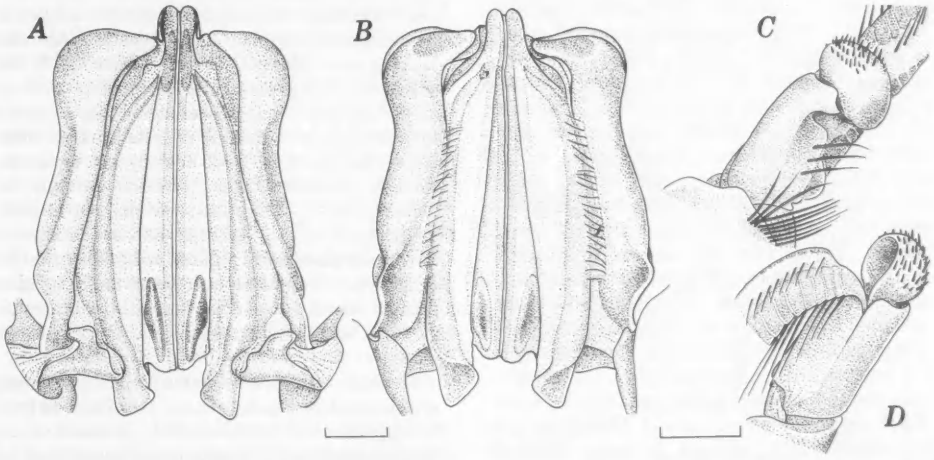

FIGURE 32.—*Penaeopsis serrata*, ♂ 22 mm cl, Golfo de los Mosquitos, Panama. *A*, Petasma, dorsal view. *B*, Ventral view. *C*, Right appendix masculina, dorsal view. *D*, Mesial view. Scales = 1 mm.

ing crest; rib of dorsolateral lobule terminating proximally in flattened subrectangular process. Ventrolateral lobule with distolateral portion broadly rounded, its rather flexible marginal part narrow and turned inwardly; ventral costa curving abruptly dorsomesially and ending in relatively broad process (with interior surface excavate) reaching approximately to level of cincinnuli; costa bearing ventral (inner) row of setae along attached margin.

Appendix masculina (Figure 32*C*, *D*) considerably broader than long (width 1.7 to almost twice length), subelliptical, convex mesially, flat laterally, and bearing mesial patch of setae.

Petasmal endopods becoming joined in male 12 mm cl. Armature of sternites XIII and XIV in very small juvenile male (discussed on p. 723) illustrated in Figure 33.

Thelycum (Figure 34) with anterior border of plate of sternite XIV slightly to strongly inclined posterolaterally, broadly arched on each side of posteromedian projection of sternite XIII; plate of sternite XIV with anterolateral extremities produced laterally into lobules of variable lengths, and lateral portions setose and raised (ventrally), slanting dorsomesially toward corresponding, narrow, submedian depression; median ridge usually ovoid or tear-shaped, sometimes subtriangular, greatly raised except for short, low, anterior part abutting projection of sternite XIII, and naked posteriorly; posterior thoracic ridge also lacking setae. Median plate of sternite XIII broad, subsemicircular, cordiform or roughly pentagonal, with transverse depression across its entire width, bearing or lacking minute anteromedian spine, and covered with densely set setae anteriorly; posteromedian projection strongly developed, broad, with posterior margin slightly emarginate to deeply bifid and studded with numerous posteriorly pointed setae. Sternite XII bearing posteromedian subconical tooth, its apex pointed ventrally or anteroventrally; oblique pair of ridges extending posterolaterally from base of tooth.

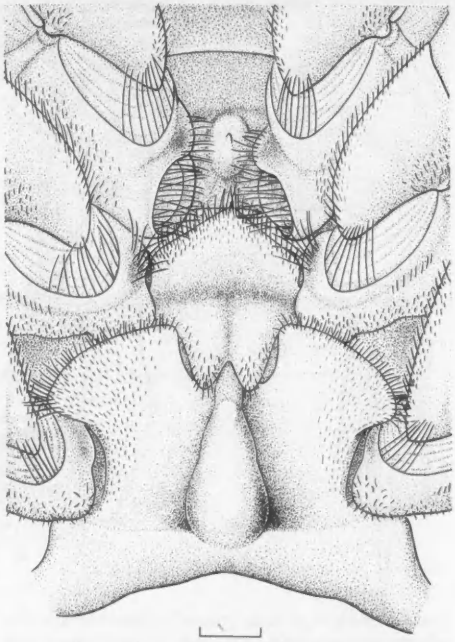

FIGURE 34.—*Penaeopsis serrata*, ♀ 29.5 mm cl, Dry Tortugas Islands, Florida. Thelycum, ventral view. Scale = 1 mm.

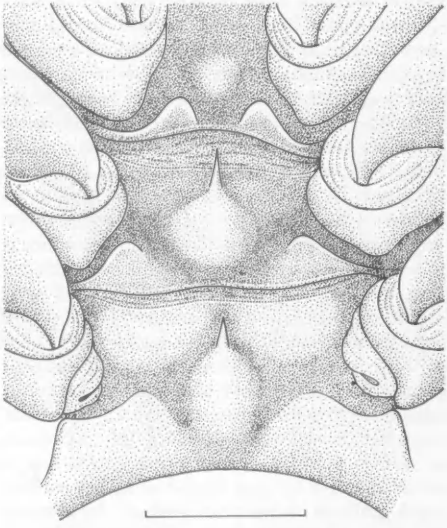

FIGURE 33.—*Penaeopsis serrata*, ♂ 10 mm cl, NE of Puerto Rico. Somites XII-XIV, ventral view. Scale = 1 mm.

Seminal receptacles (Figure 35*A*, *B*) consisting of paired bilobed membranous sacs, derived from invaginations of sternite XIV. Submedian sac large, extending posteriorly to rather near caudal margin of sternite XIV, other smaller one extending laterally; both diverging from broad an-

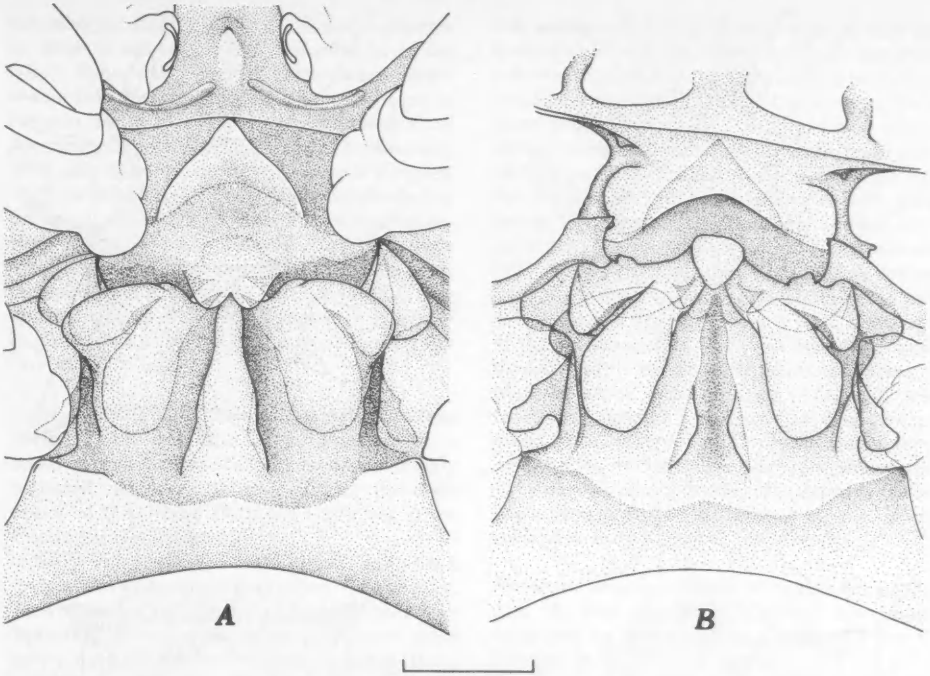

FIGURE 35.—*Penaeopsis serrata*, ♀ 30 mm cl, N of Thunder Knoll, off Honduras. Sperm receptacles. *A*, Ventral view. *B*, Dorsal view (specimen stained). Scale = 2 mm.

teromedian sinus. Receptacles opening through long, paired slits located between sternites XIII and XIV, and separated by narrow, shallow, anteromedian portion of sternite XIV.

Stages in development of thelycum: in female 8 mm cl (Figure 36*A*), plate of sternite XIV bearing median ridge produced anteriorly in long, sharp spine not quite reaching sternite XIII; anterolateral portions ventrally convex, covering invaginations (seminal receptacles) from slitlike openings along anterior margin of plate. Sternite XIII with small triangular median plate produced in long, sharp anteromedian spine reaching margin of sternite XII. Sternite XII bearing minute, sharp posteromedian tooth and pair of ridges extending posterolaterally from base of tooth (tooth and ridges changing little except increasing in size to facies in adult).

In female 9.5 mm cl (Figure 36*B*), plate of sternite XIV with spine proportionately smaller than that in few preceding instars, farther removed from sternite XIII; anterolateral portions with openings of seminal receptacles enlarged and still exposed. Sternite XIII with spine on median plate distinctly overreaching sternite XII.

In female 10.5 mm cl (Figure 36*C*), plate of sternite XIV with median ridge virtually reaching sternite XIII and bearing no more than rudiment of spine; anterolateral portions overlapping sternite XIII mesially, obscuring openings of sperm receptacles, and frequently produced laterally in short lobules, continuous with well-defined, exposed hoods. Median plate of sternite XIII with spine still slightly overreaching sternite XII.

In female 12.5 mm cl (Figure 36*D*), plate of sternite XIV with elongate trapezoidal (usually becoming tear-shaped with increasing size) median ridge, reaching sternite XIII; basal part of ridge with strong median elevation; anterolateral portions broadly overlapping sternite XIII and bearing prominent lobules partly obscuring hoods. Median plate of sternite XIII considerably broadened, its anteromedian spine minute and far removed from sternite XII; plate produced in

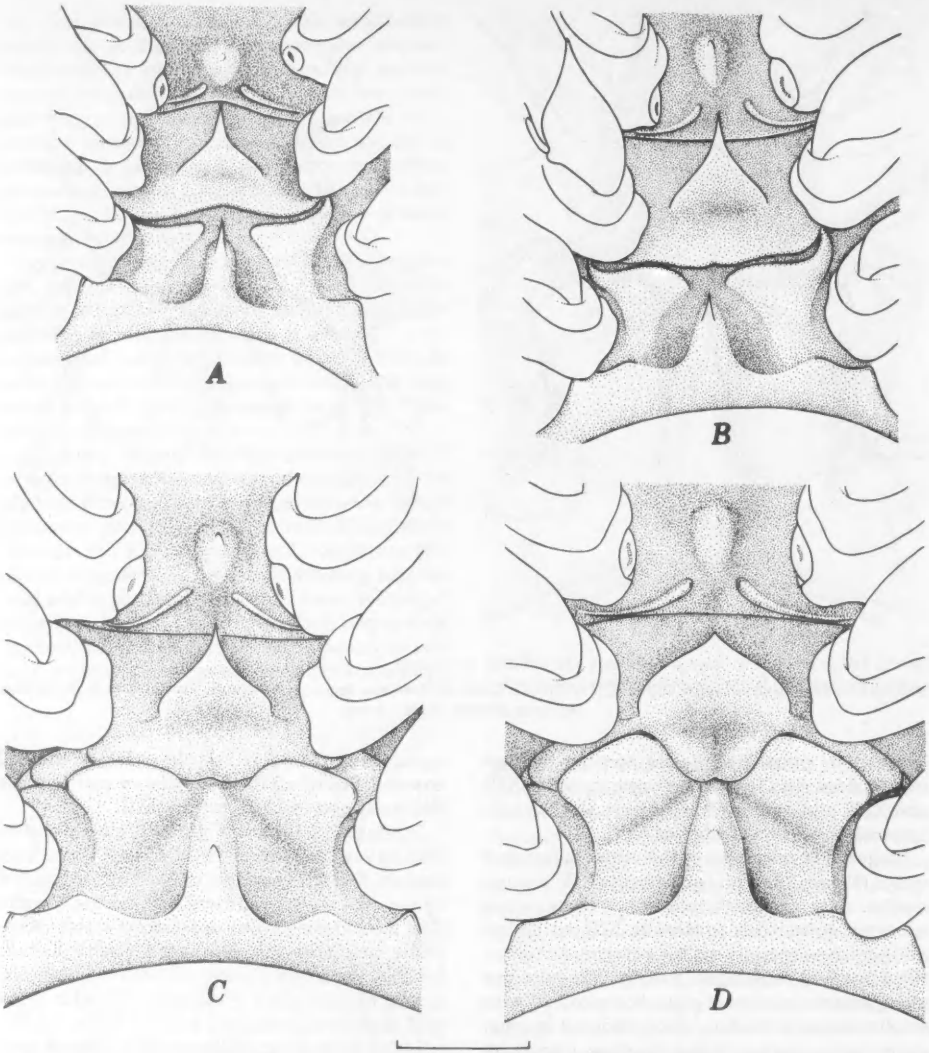

FIGURE 36.—*Penaeopsis serrata*. Stages of development of thelycum in juvenile females. *A*, 8 mm cl; *B*, 9.5 mm cl; *C*, 10.5 mm cl; *D*, 12.5 mm cl. All from W of Cartagena, Columbia. Scale = 1 mm.

broad posteromedian projection markedly overlapping sternite XIV.

In *P. serrata* the spermatophore does not bear the mesially attached element which in impregnated females of *P. balssi*, *P. eduardoi*, *P. jerryi*, and *P. rectacuta* (i.e., all the Indo-West Pacific species except *P. challengeri* of which I have not examined females carrying spermatophores) lies exposed on the thelycum. Because of the absence of this element, impregnated females of the former species are not readily recognized. The presence of a certain accessory structure in the sper-

matophore of one species of a genus and its absence in others is not unique in *Penaeopsis*; for in the family Penaeidae a similar phenomenon occurs even within the species of a subgenus. In the genus *Penaeus*, for instance, of the eight species of the American subgenus *Farfantepenaeus* Burukovsky 1972, only one, *Penaeus (F.) brevirostris* Kingsley 1878, exhibits a large, fleshy structure attached to the sperm sac which in impregnated females entirely covers the plate of sternite XIV, much like the comparable accessory element of the spermatophores of *P. rectacuta* and *P. eduardoi*. The spermatophores of the remaining seven species of *Farfantepenaeus* lack such a membranous structure.

Color.—This is one of the most beautifully colored shrimp I have seen. The following description is based on observations of a large number of freshly collected specimens obtained during the 1969 cruise of the *Oregon II* in the Caribbean (from Puerto Rico to Antigua).

Body varying from translucent light pink (sometimes with salmon hue) to deep reddish pink, interrupted by an iridescent violet to purple subelliptical patch on gastric region and various other white, deep red, violet or purple markings (lines, bands, patches, dots) on other areas. In many individuals, rostrum with numerous red chromatophores and red tip. Carapace bearing small patch of red chromatophores at base of antennal spine; anterior cardiac region with narrow, deep violet arc or transverse band running ventrally and followed by median, reddish purple subrectangular area. Some coloration continuing laterally in short posterior band, then broadening abruptly on branchiostegites, extending ventrally to margin of carapace and anteriorly to hepatic sulcus; subrectangular area flanked by white band running anteriorly to hepatic region; posterior portion of carapace white. In other individuals entire branchiostegites of highly iridescent, deep reddish pink or reddish purple. Abdominal somites with transverse reddish to purple band along posterior margin of terga; band often divided by narrow white stripe extending along dorsal midline; anterodorsal extremities of pleura bearing brilliant red or purple spot forming striking paired rows; pleura of first five somites marked by reddish to purple marginal line; bearing larger median spot and, occasionally, narrow angular stripe extending from anterodorsal spot on pleuron to median spot of same color as line; sixth somite bordered only posteriorly by line of same color as that on margin of pleura of preceding somites. Telson with paired ribs and lateral margins reddish to purple, sometimes also fixed spines and line joining their bases similarly colored. Ocular peduncle white with red stripe along margin of cornea; basal article bearing large, brilliant red or deep purple circle. Antennular peduncle highly iridescent pink proximally becoming increasingly reddish distally; distal and sometimes lateral margins of articles red or purple; flagella pink or reddish, fading distally; frequently ventral flagellum white and dorsal reddish. Antennal flagella pink. Pereopods of lighter shade than body, but lateral surfaces usually darker and strongly iridescent. Bases of pleopods white, light pink, or violet with posterolateral surfaces iridescent with deep pink or violet hues; endopods and exopods translucent, and bearing reddish or purplish spot proximally. Uropods with lateral portion of protopod of darker shade than mesial; rami usually of same or lighter color than body but deeper proximally.

Maximum lengths.—Males 120 mm tl; female 150 mm tl (Maurin 1952). Largest specimens examined by me: males 24 mm cl, 112 mm tl; females 34.5 mm cl, 135 mm tl.

Geographic and bathymetric ranges (Figure 37).—Western Atlantic: from east of Barnegat, N.J., south of Martha's Vineyard, Mass. (lat. 40°00′ N, long. 70°47′ W, coordinates from Haedrich et al. 1975, *Gosnold* cruise 197, stn 111), through the Gulf of Mexico and the Caribbean south to French Guiana (lat. 7°11′ N, long. 52°58′ W). Also found at a disjunct locality, off Rio Grande do Sul (lat. 32°45′24″S, long. 50°24′00″W). The record from off Barnegat, which represents the most northerly point at which this shrimp has been found, and that off Rio Grande do Sul, marking the southernmost record of the occurrence of the species, were both reported by Pérez Farfante and Ivanov (1979).

Eastern Atlantic: from south of Cabo San Vicente, Portugal, to off Cadiz, Spain (Maurin 1961, 1965) and off the northwest coast of Africa to Tamzak ("Tamxat") (lat. 17°26′ N, long. 16°03′ W), Mauritania (Maurin 1968b).

In the western Atlantic, *Penaeopsis serrata* frequents depths between 183 and about 750 m (records of its presence in shallower water are almost certainly erroneous), with maximum concentrations occurring from 300 to 450 m. In the eastern

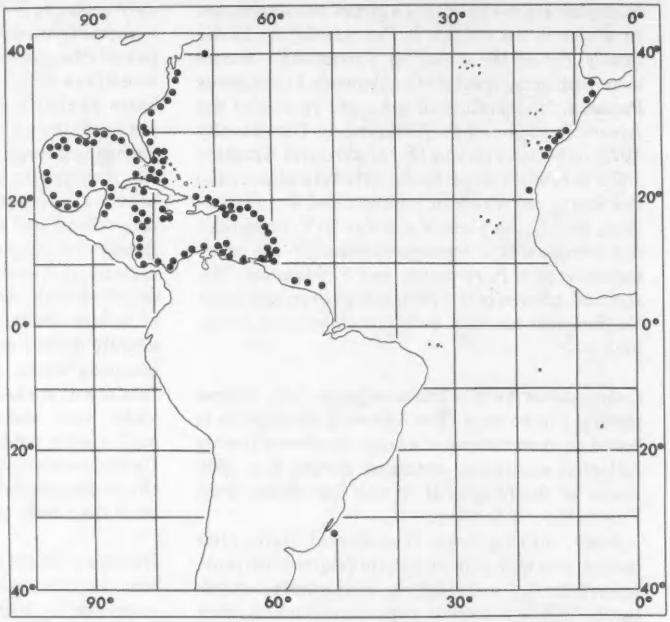

FIGURE 37.—Range of *Penaeopsis serrata* based on published records and specimens personally examined.

Atlantic it has been reported between 120 (Lagardère 1971) and 700 m (Maurin 1961).

The temperature-depth relationship for *P. serrata* is presented in Figure 38. In three areas, two in the Gulf of Mexico and one in the southern part of the Caribbean (off Venezuela), this shrimp shows similar ranges of temperature and depth. In the northeast Gulf, however, the range is apparently more extensive, the animals having penetrated shallower and warmer as well as deeper and colder waters. According to the available data, the population off the southeast coast of the United States occurs within the shallower range depths occupied by other populations, but at lower temperatures. Actually, in that area the shrimp is not restricted to the depths presented in the graph,

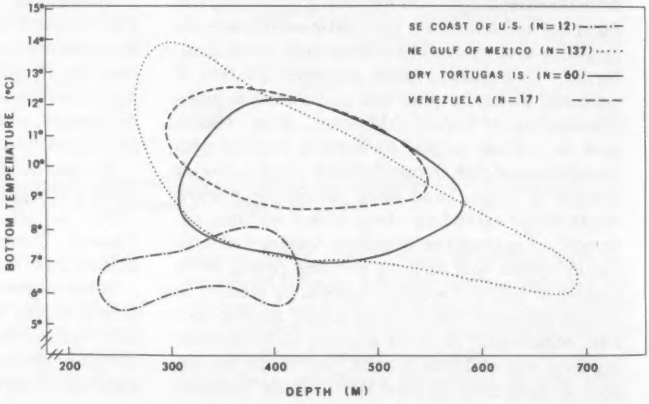

FIGURE 38.—Depth-temperature relationships for *Penaeopsis serrata* in four western Atlantic areas (data obtained from *Oregon* and *Oregon II* Station Lists).

because in at least one locality (for which temperature data are lacking) it has been found at about 550 m (see "Material" herein), i.e., only 150 m above the maximum depth at which it has been taken in the northeast Gulf. Because the temperature-depth distribution of the population off the southeast coast of the United States is based on only 12 records, one may only point out the unusual conditions existing in this segment of the range of *P. serrata*. According to my observations, the specimens of that population exhibit no morphological differences from those of other localities throughout the broad range of the species, but Harvey R. Bullis Jr.[4] stated that the specimens, observed by him immediately after capture, had a different coloration from those caught elsewhere. Furthermore, Bullis and Rathjen (1959) found that off the southeast coast of the United States *P. serrata* was most abundant at slightly greater depths than *Pleoticus robustus* (Smith 1885), whereas in all other areas megalops was not abundant where it occurs with, or at shallower depths than, *P. robustus*.

Variation.—This species, like most members of the genus, exhibits a large number of characters that are highly variable. Among them, the rostrum, strongly arched in the young, may be straight, arcuate only basally or sinuous in the adult, and horizontal or upturned; the number of rostral teeth ranges from 10 to 19. The scaphocerite may fall short of or surpass the distal end of the antennular peduncle, and the mesial ramus of the uropod may not reach the apex of telson or may extend beyond it by as much as 0.15 of its own length. The thelycal features, especially, show a wide range of variation: the anterior border of the plate of sternite XIV, usually strongly arched on each side of the posteromedian projection of sternite XIII, sometimes is moderately or only slightly so; and the anterolateral lobules of that plate although generally strongly developed are sometimes quite short. The median plate of sternite XIII varies in shape (from subsemicircular to roughly pentagonal), while the posteromedian projection, although always broad, may range from slightly emarginate to deeply bifid. The entire range of variations in some of the characters cited have been observed in animals from the same locality.

[4]Harvey R. Bullis, Jr., formerly Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. December 1978.

At least in the western Atlantic populations, there are also differences in the relative extension of the third maxilliped and pereopods. I have noticed that in the populations of the Caribbean and Atlantic coast of South America they extend distally slightly farther than they do in northern populations. In the former populations the range extension of these appendages falls within the upper half of the limits cited herein and in the northern ones within the lower half. Because most of the few specimens available to me from the eastern Atlantic are poorly preserved, I have been unable to arrive at definite conclusions as to the relative length of the appendages in the populations occurring in that region.

Affinities.—*Penaeopsis serrata*, the only Atlantic member of the genus, differs from its congeners in that the branchiocardiac carina and interrupted cicatrix on the sixth abdominal somite are very weak, and the knob at the distal end of the semicircular part of the ventral antennular flagellum in the male is rather inconspicuous. More strikingly, it differs from its allies in a number of features of the external genitalia, as pointed out below. It appears to be closer to *P. rectacuta* than to any of the other species. They share long rostra which tend to possess a large number of teeth (up to 18 in *P. serrata* and 17 in *P. rectacuta*), and the second tooth is located at the level of the orbital margin. In both, the hepatic spine is situated ventral to the level of the antennal spine, and the branchiocardiac carina does not approach closely the hepatic sulcus. The petasmata are also rather similar and the telson of *P. serrata* is sometimes, although rarely, armed with three pairs of movable spines as is typical of that of *P. rectacuta*.

The thelyca exhibit the most obvious differences between the two species. In *P. serrata* the plate of sternite XIV is uniquely produced into laterally directed lobules, bears an entirely naked and much stronger median ridge (usually subovoid instead of flasklike as it is generally in *P. rectacuta*), and the posterior thoracic ridge lacks setae across its anterior border. Furthermore, in *P. serrata* the median plate of sternite XIII, although variable in shape, is generally semicircular or roughly pentagonal, whereas in *P. rectacuta* it is cordiform. The posteromedian projection of sternite XIII is also broader and emarginate (often deeply) rather than entire as it usually is in *P. rectacuta*. The males of these species can also be distinguished by the proximal plate of the dorsomedian lobule of the

petasma which in *P. serrata*, although thickened mesially, does not form a sharp crest as it does in *P. rectacuta*; by the proximal plate of the dorsolateral lobule subrectangular in the former and nearly circular in the latter; and by the apical process of the ventral costa which is conspicuously broader in *P. serrata* than in *P. rectacuta*.

Remarks.—With reference to the types of this species, both Bate (1881) and A. Milne Edwards considered the account of *P. serratus* included in the A. Milne Edwards' manuscript—later published jointly by A. Milne Edwards and Bouvier (1909)—to constitute the original description; therefore, it seems reasonable to me that the syntypes of this species, from Barbados, designated by A. Milne Edwards and Bouvier are, by implication, also those of Bate. Furthermore, Bate (1881:180) stated that "I have not had an opportunity of examining the branchial apparatus to feel quite certain that the genus [*Penaeopsis*] is a good determination," thereby indicating that he had not examined any specimens of *P. serrata*.

Commercial importance.—Extensive explorations in the Gulf of Mexico, the Caribbean, and along the northern coast of South America by the U.S. Government vessels *Oregon* and *Oregon II* demonstrated the occurrence of megalops in many areas on the upper slope of the continental and insular shelves. It is common in many localities, and, on the basis of collections made by the RV *Alaminos*, Roberts and Pequegnat (1970) stated that this shrimp "is the most abundant penaeid caught by the *Alaminos* in the Gulf, and it appears to be most abundant in the De Soto Canyon around 200 fathoms [366 m] and, secondarily, off the Rio Grande in 150 fathoms [274 m]." Even though it is frequently taken while trawling for the royal red shrimp, *Pleoticus robustus* (Smith 1885), Harvey R. Bullis, Jr. (see footnote 4) has informed me that no serious effort was made during the cruises of the *Oregon* and *Oregon II* to assess the commercial potential of *P. serrata*. The reason for lack of interest in investigating possibilities for commercial exploitations was the small size of this shrimp—according to Bullis, the average count of megalops tails would have been in the range of 60-100/lb (132-220/kg). In the eastern Atlantic this species constitutes a part of the commercial catches: Maurin (1952) cited it as one of the shrimps commercially fished off Morocco at depths >200 m; I have examined two females sorted by L. B. Holthuis from commercial catches made by a Cadiz trawler off Rabat, Morocco; and Holthuis and Rosa (1965) listed it among the shrimps of economic value in the "Southeast Atlantic Area."

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LIKELIHOOD METHODS FOR THE VON BERTALANFFY GROWTH CURVE

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ABSTRACT

Likelihood methods for the von Bertalanffy growth curve are examined under the assumption of independent, normally distributed errors. The following are examined: determining the best method of estimation, relationships between methods of estimation, failure of assumptions, constructing confidence regions, and applying likelihood ratio tests. An example is presented illustrating many of the methods discussed in theory.

The paper may be viewed as an application of classic nonlinear least squares methods to the von Bertalanffy curve. As such, the concepts discussed are generally applicable and the paper may serve as an introduction to nonlinear least squares.

Since the application of the von Bertalanffy (1938) growth curve by Beverton and Holt (1957) to the yield per recruit problem, this curve has been widely used in fisheries biology. The original curve has been generalized (Richards 1959; Chapman 1961). However, this paper will not deal with the more general Chapman-Richards growth curve. Nor will it deal with the biological motivation for these curves which have been discussed by the cited authors. Instead, I confine my study to the classic von Bertalanffy curve and examine what appears to be reasonable methods for the statistical treatment of data.

THE MODEL AND ITS MAXIMUM LIKELIHOOD ESTIMATES

I assume that age-length data are available on some species, and that the relationship between age and length can be adequately described by the von Bertalanffy growth curve. Using the usual notation, the length of the uth individual of age t_u is assumed to be

$$\begin{aligned} l_u &= l_\infty(1-\exp(-K(t_u-t_0))) + \epsilon_u \\ &= \mu(l_\infty, K, t_0, t_u) + \epsilon_u \\ &= \mu(t_u) + \epsilon_u \end{aligned}$$

where l_∞ is asymptotic length, K a constant describing how rapidly this length is achieved, t_0 the hypothetical age at length zero, and the ϵ_u's independent $N(0,\sigma^2)$ random variables.

For this model, parameters can best be estimated using the method of maximum likelihood. The principal reasons why maximum likelihood estimates are desirable are that under very general conditions (much more general than described here) they are consistent (converge in probability to the correct value), asymptotically normal, and asymptotically attain (except under unusual circumstances) the smallest possible variance. It will not be necessary to expand on these properties because they are among the most important results in statistics, and are discussed to some extent in virtually every book on mathematical statistics.

Letting $S(l_\infty,K,t_0) = \Sigma_u(l_u-\mu(l_\infty,K,t_0,t_u))^2$, the likelihood function can be written as

$$\begin{aligned} &\ell(l_\infty, K, t_0, \sigma^2) \\ &\quad = (2\pi\sigma^2)^{-N/2} \exp(-S(l_\infty, K, t_0)/2\sigma^2) \quad (1) \end{aligned}$$

where N is the number of observations. Since for any given value of σ^2, say σ_0^2, $\ell(l_\infty,K,t_0,\sigma_0^2)$ is maximized when $S(l_\infty,K,t_0)$ is minimized, it follows that the maximum likelihood (ML) estimates of (l_∞,K,t_0), say $(\hat{l}_\infty,\hat{K},\hat{t}_0)$, are the least squares (LS) estimates. These estimates shall be referred to as ML or LS depending on the property which is being emphasized.

The ML estimate of σ^2 is obtained in the usual way by first taking the log likelihood, calculating the partial derivative with respect to σ^2, and setting this result equal to zero

$$\begin{aligned} &\log(\ell(l_\infty, K, t_0, \sigma^2)) \\ &\quad = -(N/2)\log(2\pi\sigma^2) - S(l_\infty, K, t_0)/2\sigma^2 \end{aligned}$$

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$$\frac{\partial \log(\mathcal{L}(l_\infty, K, t_0, \sigma^2))}{\partial \sigma^2}$$

$$= -N/2\sigma^2 + S(l_\infty, K, t_0)/2(\sigma^2)^2 = 0$$

$$\hat{\sigma}^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/N .$$

Thus the problem of ML estimation for the von Bertalanffy curve reduces to finding LS estimates of (l_∞, K, t_0). Note that this is a general property of the normal error model, since no special properties of the von Bertalanffy curve have been used.

The normal equations for finding ML estimates are obtained by taking the partial derivative of $S(l_\infty, K, t_0)$ with respect to the unknown parameters and setting the results equal to zero (i.e., $\partial S/\partial l_\infty = 0$; $\partial S/\partial K = 0$; $\partial S/\partial t_0 = 0$). Because these equations do not allow a simple solution, the graphical Ford-Walford method (Ricker 1975; actually the regression of l_{t+1} on l_t) has been widely used. The Ford-Walford plot, in addition to a plot of average length at age, should be adequate for determining the age range following the von Bertalanffy curve.

For the von Bertalanffy curve, proper ML estimates can only be found using iterative algorithms. A number of authors (Stevens 1951; Tomlinson and Abramson 1961; Allen 1966) have suggested specialized algorithms. Although these algorithms may have advantages when computers are not available, the easiest way to obtain ML estimates is to use any of the general purpose nonlinear LS computer programs available in BMD (Dixon 1976), BMDP (Dixon 1977), or SPSS (Nie et al. 1975). These programs have the flexibility of allowing complicated curves to be fit to data sets, which is especially useful if differences in growth curves among different populations are to be tested statistically. For example, it might be necessary to fit different growth curves to several populations, but with the constraint that the t_0's be equal.

It should be remembered that LS solutions obtained iteratively may be local rather than global minimizations of $S(l_\infty, K, t_0)$. With this in mind, initial values provided to any iterative procedure must represent the best available information. I recommend that the Ford-Walford method be used to calculate initial values. This guarantees that any LS solution which is obtained has smaller residual sum of squares than the Ford-Walford estimates.

LEAST SQUARES METHODS OF ESTIMATION

Under differing assumptions on the error variance, four different LS methods of estimation are appropriate. When these assumptions are met, each method provides ML estimates under the likelihood model (Equation (1)).

Let l_{ij} be the length of the jth individual of age t_i, and let $\bar{l}_i$ and s_i^2 be the sample mean and sample variance of the lengths of individuals of age t_i, based on a sample size n_i. For each method, the assumption on the error variance and the appropriate sum of squares to be minimized when this assumption is correct, is given below.

(a) All l_{ij} have constant variance:

$$\Sigma(l_{ij} - \mu(t_i))^2 .$$

(b) All $\bar{l}_i$ have constant variance:

$$\Sigma(\bar{l}_i - \mu(t_i))^2 .$$

(c) The variance of l_{ij} varies with t_i, and at age t_i is equal to σ_i^2:

$$\Sigma(n_i/s_i^2)\,(\bar{l}_i - \mu(t_i))^2 .$$

(d) All l_{ij} have constant variance (i.e., the same assumption as (a) above):

$$\Sigma n_i(\bar{l}_i - \mu(t_i))^2 .$$

The dependent variables in methods (a) and (b) are formally of the form described by the likelihood model (Equation (1)). By this it is meant that they have constant variance, and assuming normality and independence, their likelihood is described by Equation (1). The dependent variables in methods (c) and (d) can be transformed into the form of Equation (1). This can be done by placing the weights $w_i = (n_i/s_i^2)$ (method (c)) and $w_i = n_i$ (method (d)) within the squared expressions. Doing so for method (c) gives the pseudoobservation $y_i = (\sqrt{n_i}/s_i)\bar{l}_i$ with expectation $E(y_i) \approx (\sqrt{n_i}/s_i)\mu(t_i)$ and variance asymptotically equal to unity (as $s_i \to \sigma_i$). Assuming normality and independence, the asymptotic likelihood of these y_i is described by Equation (1). Similarly for method (d), the pseudoobservation becomes $y_i = (\sqrt{n_i})\bar{l}_i$ with expectation $E(y_i) = (\sqrt{n_i})\mu(t_i)$ and variance σ^2. Again assuming normality and inde-

pendence, the likelihood of these y_i is described by Equation (1). It follows that likelihood procedures applicable to unweighted methods (a) and (b) are also applicable to weighted methods (c) and (d) with few modifications. These arguments apply when fitting any function using LS estimation.

Selection of an appropriate LS method for a given problem can largely be made on the validity of the error assumption, but not solely on this basis. It is also useful to keep in mind the purpose of fitting the curve. For example, a curve fit with method (a) would do well in predicting the length of a randomly selected individual (if data were from random samples), and this property would be important in, say, modeling applications. Method (b), on the other hand, may best describe the growth of a species over its entire lifespan, a property which would be desirable when comparing growth among species. It should be noted that the practice of graphing the estimated curve and plotting average lengths observed at each age is visually biased toward method (b). Method (b) will generally look best on this type of plot.

Method (c) is appropriate when it is apparent that the variance at each age varies significantly. This assumption can be examined using Bartlett's or Cochran's tests (Dixon and Massey 1957) for the homogeneity of variance.

Method (d) is largely a computational device. In the following section it is shown that method (d) is nearly equivalent to method (a), but often requires much less computational effort.

NEAR EQUIVALENCE OF METHODS (A) AND (D)

Calculations for method (a) can be performed using method (d), with often a large savings in computational effort. It will be shown that methods (a) and (d) yield identical parameter estimates, and similar covariance matrix estimates of parameter estimates. These results are general properties of LS estimates under the assumptions of method (a), and are not dependent on the form of the function being fitted.

Identity of Parameter Estimates

For the von Bertalanffy curve using method (a), the sum of squares to be minimized is

$$S(l_\infty, K, t_0) = \sum_i \sum_j (l_{ij} - \mu(l_\infty, K, t_0, t_i))^2 .$$

The sum of squares to be minimized using method (d) is

$$S_w(l_\infty, K, t_0) = \sum_i n_i(\bar{l}_i - \mu(l_\infty, K, t_0, t_i))^2 .$$

The normal equation is derived for the parameter K say, using method (a), by taking the partial derivative of S with respect to K and setting the result equal to zero:

$$\frac{\partial S}{\partial K} = \sum_i \sum_j -2(l_{ij} - \mu(t_i))\mu_K'(t_i)$$

$$= -\sum_i 2\mu_K'(t_i) n_i(\bar{l}_i - \mu(t_i)) = 0 .$$

The normal equation is obtained for method (d) by taking the partial derivative of S_w with respect to K, yielding a result identical to that from method (a):

$$\frac{\partial S_w}{\partial K} = -\sum_i 2\mu_K'(t_i) n_i(\bar{l}_i - \mu(t_i)) = 0 .$$

Because this identity of the two normal equations is not due to any special property of K, normal equations obtained from methods (a) and (d) are identical, implying corresponding LS estimates are also identical.

Similarity of Covariance Matrix estimates

The asymptotic covariance matrix for parameters $\theta' = (\theta_1, \ldots, \theta_p)$ estimated using ML theory is the inverse information matrix $I(\theta)^{-1}$ (Kendall and Stuart 1973), where $I(\theta) = (I_{ij})$,

$$I_{ij} = -E\frac{\partial^2 L(\theta, X)}{\partial\theta_i \partial\theta_j} ,$$

$L(\theta, X) = \log(\ell(\theta, X))$, and $\ell(\theta, X)$ is the likelihood function.

For nonlinear LS estimates, $I(\theta)^{-1}$ can be estimated using

$$\hat{\Sigma} = (Z'Z)^{-1} s^2$$

which is the formula used by nonlinear LS computer programs. Generally, $Z = (Z_{ij})$, where Z_{ij} is the partial derivative of the expectation of the ith observation with respect to the jth parameter

evaluated at the ML estimates, and s^2 is the mean square error.

For estimates calculated using method (a),

$$Z' = \begin{bmatrix} \frac{\partial\mu(t_1)}{\partial l_\infty}, \ldots, \frac{\partial\mu(t_1)}{\partial l_\infty}, \ldots, \frac{\partial\mu(t_I)}{\partial l_\infty}, \ldots, \frac{\partial\mu(t_I)}{\partial l_\infty} \\ \frac{\partial\mu(t_1)}{\partial K}, \ldots, \frac{\partial\mu(t_1)}{\partial K}, \ldots, \frac{\partial\mu(t_I)}{\partial K}, \ldots, \frac{\partial\mu(t_I)}{\partial K} \\ \frac{\partial\mu(t_1)}{\partial t_0}, \ldots, \frac{\partial\mu(t_1)}{\partial t_0}, \ldots, \frac{\partial\mu(t_I)}{\partial t_0}, \ldots, \frac{\partial\mu(t_I)}{\partial t_0} \end{bmatrix} \quad 3\times N$$

evaluated at $(\hat{l}_\infty,\hat{K},\hat{t}_0)$, with $s^2 = S(\hat{l}_\infty,\hat{K},\hat{t}_0)/(N-3)$, $N = \Sigma_i\, n_i$ and I the number of age categories.

As was previously noted for method (d), it is often advantageous to view this model as being unweighted with transformed variables. From this point of view, $y_i = (\sqrt{n_i})\bar{l}_i$ is the dependent variable, with expectation $E(y_i) = (\sqrt{n_i})\mu(t_i)$. Under this parameterization, $\text{var}(y_i) = \sigma^2$ with

$$Z_w' = \begin{bmatrix} \sqrt{n_1}\,\frac{\partial\mu(t_1)}{\partial l_\infty}, \ldots, \sqrt{n_I}\,\frac{\partial\mu(t_I)}{\partial l_\infty} \\ \sqrt{n_1}\,\frac{\partial\mu(t_1)}{\partial K}, \ldots, \sqrt{n_I}\,\frac{\partial\mu(t_I)}{\partial K} \\ \sqrt{n_1}\,\frac{\partial\mu(t_1)}{\partial t_0}, \ldots, \sqrt{n_I}\,\frac{\partial\mu(t_I)}{\partial t_0} \end{bmatrix} \quad 3\times I$$

again evaluated at $(\hat{l}_\infty,\hat{K},\hat{t}_0)$, with $s_w{}^2 = S_w(\hat{l}_\infty,\hat{K},\hat{t}_0)/(I-3)$.

It is easily verified that $Z'Z = Z_w'Z_w$ and, therefore, any differences in the covariance matrix estimates of parameter estimates must be due to differences in the estimates s^2 and $s_w{}^2$ of σ^2. Although s^2 provides a better estimate than $s_w{}^2$ in terms of degrees of freedom ($N-3$ versus $I-3$), they should be similar in value, and hence it can be expected that methods (a) and (d) provide similar covariance matrix estimates of parameter estimates.

This analysis points out that good estimates of the covariance matrix of parameter estimates require having sufficient numbers of observations so that σ^2 is adequately estimated. From this point of view method (a) is superior to method (d). However, method (d) can be modified so that data are not completely collapsed (averaged) at each value of the independent variable. Instead, data can be partitioned so that there are several dependent variable averages, and weights, at each value of the independent variable. A similar technique can be applied to method (c).

Another possibility would be to estimate σ^2 independent of the LS calculations by pooling the $s_i{}^2$ values. However, this estimate based on pure error would tend to underestimate the true σ^2 which will often contain a lack of fit component (see the following section for a discussion concerning pure error and lack of fit).

FAILURE OF ASSUMPTIONS

There are two ways in which the assumed model can fail: 1) growth may not follow the von Bertalanffy curve; or 2) error assumptions may not hold.

Failure of the von Bertalanffy Curve

Even when growth follows the von Bertalanffy curve, expected lengths at age from sample data may not. Discrepancies can be caused by bias in sampling, bias in age determination, or size selective survival in the natural population. Because samples tend to be biased toward larger individuals, age readers tend to under-age older individuals, and larger individuals of an age group tend to have better survival, these factors may bias the observed size upward for a given age.

When a number of length specimens are available at each age, a statistical measure of lack of fit (departure from the von Bertalanffy curve) can be calculated using the procedure described by Draper and Smith (1966). For this analysis, it is

necessary to assume that the error variance of individuals is constant (i.e., the variance assumption of method (a) holds). It is also important to remember that for nonlinear models (such as the von Bertalanffy curve) the procedure is not strictly valid, but is analogous to calculations valid under linear models.

The residual sum of squares calculated using method (a) can be partitioned into a pure error component (S_{pe}) and a lack of fit components (S_{lof}). Estimates of these components are

$$S_{pe} = \Sigma(n_i-1)s_i^2$$

and $$S_{lof} = S(\hat{l}_\infty,\hat{K},\hat{t}_0)-S_{pe}\ .$$

For a linear model with no lack of fit,

$$\tilde{F} = (S_{lof}/(I-3))/(S_{pe}/(N-I))$$

would have an F-distribution with $\nu_1 = I-3$ and $\nu_2 = N-I$ degrees of freedom. While recognizing that the von Bertalanffy curve is not a linear model, this statistic may still serve as a tentative examination for lack of fit.

Even if the data show significant lack of fit, the von Bertalanffy curve may still provide the most useful growth analysis. Rejection of the von Bertalanffy curve must ultimately be based on superior alternative curves or methods of analysis.

Failure of Error Assumptions

When a number of length specimens are available at each age, parameter estimates should be robust against violations of the normality assumption. As was previously shown, estimates can be viewed as solutions to a LS problem with observations $y_i = (\sqrt{n_i})\bar{l}_i$ which are always approximately normally distributed due to the central limit theorem.

The most likely form of heteroscedasticity is the varying of variance with age. Method (c) provides an appropriate analysis for this case.

If observations are correlated, there will be no practical remedy. Efficient estimates will generally depend on the $N \times N$ correlation matrix of errors. This matrix will generally not be estimable.

CONSTRUCTING CONFIDENCE REGIONS

For method (a), confidence regions of approximate size $1-q$ around ML estimates $(\hat{l}_\infty,\hat{K},\hat{t}_0)$ can be constructed using the relationship

$$S(l_\infty,K,t_0)$$

$$= S(\hat{l}_\infty,\hat{K},\hat{t}_0)\,[1+\frac{3}{N-3}F(3,N-3,1-q)\,]$$

$$= c_q \text{ (Draper and Smith 1966)}$$

where $F(3,N-3,1-q)$ is the $(1-q)$th percentile of the F-distribution with $\nu_1 = 3$ and $\nu_2 = N-3$ degrees of freedom. That is, values of (l_∞,K,t_0) which satisfy $S(l_\infty,K,t_0) = c_q$ form a three-dimensional surface enclosing the true value of (l_∞,K,t_0) with approximate probability $1-q$. The probability level would be exactly $1-q$ if the growth model was linear, but for nonlinear models (such as the von Bertalanffy curve) this value is only approximated. Although methods exist which provide confidence regions with exact values for q (Hartley 1964), such methods are inferior to that of Draper and Smith in that they: 1) have a degree of arbitrariness in the selection of a region, 2) do not follow contours of equal likelihood, and 3) are more complex to apply.

The relationship defining a contour is

$$S(l_\infty,K,t_0)-c_q = 0$$

where $S(l_\infty,K,t_0)$

$$= \sum_u [\,l_u^2-2l_\infty l_u(1-\exp(-K(t_u-t_0)))$$

$$+ l_\infty^2(1-\exp(-K(t_u-t_0)))^2\,]$$

and $c_q = S(\hat{l}_\infty,\hat{K},\hat{t}_0)\,[1+\frac{3}{N-3}F(3,N-3,1-q)]\ .$

Therefore, $S(l_\infty,K,t_0)-c_q = Al_\infty^2 + Bl_\infty + C$

where $A = \sum_u (1-\exp(-K(t_u-t_0)))^2$

$$B = -2\Sigma l_u(1-\exp(-K(t_u-t_0)))$$

and $C = \sum_u l_u^2-c_q\ .$

Solutions exist for the three-dimensional contour problem whenever $B^2-4AC \geq 0$.

Points on the three-dimensional contour are easily calculated by conditioning on a value for t_0, and calculating the two-dimensional cross section (l_∞,K) by stepping through plausible values for K, and when $B^2-4AC \geq 0$, calculating $l_\infty = (-B \pm \sqrt{B^2-4AC})/(2A)$. By varying t_0 also, this algorithm will generate the entire three-dimensional confidence region.

Although points on the contour surface are easily calculated, the fact that three parameters are involved in the von Bertalanffy curve greatly limits the usefulness of confidence regions. This is due to the simple fact that three-dimensional regions are difficult to display.

The simplest solution to this problem is to condition on $\hat{t}_0$, and graph the resulting two-dimensional cross section (l_∞,K). It must be remembered that this region is not a true confidence region since more extreme values of (l_∞,K) may occur at a different value of t_0. Thus this procedure will give only a rough idea of our confidence in the estimates $(\hat{l}_\infty,\hat{K})$. A more time consuming solution is to graph a series of cross sections, or possibly a three-dimensional graph.

If method (b) is used to estimate parameters, the analysis follows as in method (a), by simply replacing l_u with $\bar{l}_u$ and N with I.

If weighted methods (c) or (d) is used to estimate parameters, confidence regions are defined by the relationship

$$S_w(l_\infty,K,t_0) = S_w(\hat{l}_\infty,\hat{K},\hat{t}_0)[1+\frac{3}{I-3}F(3,I-3,1-q)] = c_q' .$$

Computations proceed as in the unweighted case, but with

$$A_w = \sum_u w_u(1-\exp(-K(t_u-t_0)))^2 ,$$

$$B_w = -2\sum_u w_u \bar{l}_u(1-\exp(-K(t_u-t_0)))$$

and $$C_w = \sum_u w_u \bar{l}_u^{\,2} - c_q' .$$

For method (c) $w_u = n_u/s_u^2$, and for method (d) $w_u = n_u$.

APPLYING LIKELIHOOD RATIO TESTS

Likelihood ratio (LR) tests provide a general method for the statistical comparison of growth curves. It is a well-known and often exploited fact that once a general probability model has been specified (Ω), hypothesis tests of linear constraints on parameters in this model can be derived using the LR criterion. Alternatively viewed, linear constraints on parameters in Ω imply a simplified model ω. Tests of linear constraints on Ω are thus equivalent to testing ω against Ω.

The LR criterion can be used on the single sample problem, when it is desired to test whether a sample came from a population with some "known" values for any or all of the parameters (l_∞,K,t_0); or for the multisample problem comparing von Bertalanffy curves in different populations. The first problem will be solved by the simplest application of theory derived mainly in the context of the second problem. When a single parameter is being tested in the one or two sample problem, it makes good sense to simply use a Z-statistic (since ML estimates are asymptotically normal) and forego the more extensive calculations required for LR tests. One advantage that the Z test has over the LR test for the two sample problem is that σ^2 does not need to be equal in the two populations.

Consider I different populations each following the von Bertalanffy curve with parameters $(l_{\infty i},K_i,t_{0i})$, $i = 1,\ldots,I$. These populations would typically be the same species in different habitats, males and females, etc. Let l_{ij} be the length of the jth observation in the ith population, of age t_{ij}, $j = 1,\ldots,n_i$, $N = \Sigma_i n_i$, with variance σ^2 independent of i. Note that the meaning of subscripts has been changed from what was used in previous sections.

Letting $S(l_\infty,K,t_0) = \Sigma_i\Sigma_j(l_{ij}-\mu(l_{\infty i},K_i,t_{0i},t_{ij}))^2$, the likelihood function under (Ω) can be written as

$$\ell(l_\infty,K,t_0,\sigma^2) = (2\pi\sigma^2)^{-N/2}\exp(-S(l_\infty,K,t_0)/2\sigma^2)$$

where $l_\infty' = (l_{\infty 1},\ldots,l_{\infty I})$,
$K' = (K_1,\ldots,K_I)$,
and $t_0' = (t_{01},\ldots,t_{0I})$.

Although the above parameterization is appropriate for unweighted methods (a) and (b), the reader can verify that no additional problems arise using weighted methods (c) and (d).

Previously, it was shown that likelihood functions of the form $\ell(l_\infty,K,t_0,\sigma^2)$ are maximized by LS estimates $(\hat{l}_\infty,\hat{K},\hat{t}_0)$, with the ML estimate of σ^2 being

$$\hat{\sigma}^2 = S(\hat{l}_\infty, \hat{K}, \hat{t}_0)/N.$$

This is true whether or not there are any linear constraints placed on the parameters being estimated. Substituting $\hat{\sigma}^2$ into $\mathcal{L}(l_\infty, K, t_0, \sigma^2)$ yields the maximum value of the likelihood function

$$\max\left(\mathcal{L}(l_\infty, K, t_0, \sigma^2)\right) = (2\pi\hat{\sigma}^2)^{-N/2} \exp(-N/2).$$

The LR for the hypothesis

H_ω: that the parameters (l_∞, K, t_0) satisfy some set of r linear constraints, say R

against the alternative

H_Ω: that the parameters (l_∞, K, t_0) possibly satisfy no linear constraints

$$\text{is } \Lambda = \frac{\max\left(\mathcal{L}(l_\infty, K, t_0, \sigma^2)\right), R}{\max\left(\mathcal{L}(l_\infty, K, t_0, \sigma^2)\right)}.$$

$$(l_\infty, K, t_0)$$

Letting $\hat{\sigma}^2_\omega$ and $\hat{\sigma}^2_\Omega$ be the ML estimates of σ^2 under ω and Ω, respectively, this LR becomes

$$\Lambda = \frac{(2\pi\hat{\sigma}^2_\omega)^{-N/2} \exp(-N/2)}{(2\pi\hat{\sigma}^2_\Omega)^{-N/2} \exp(-N/2)} = (\hat{\sigma}^2_\Omega / \hat{\sigma}^2_\omega)^{N/2}.$$

Under H_ω, the test statistic $-2 \log(\Lambda) = -N \log(\hat{\sigma}^2_\Omega/\hat{\sigma}^2_\omega)$ will have asymptotically a X^2_r distribution. A derivation of this distribution given by Kendall and Stuart (1973) can be modified to accommodate the present model.

Because LR tests are based on statistics having asymptotically a X^2_r distribution, the validity of this test is dependent on the sample sizes used in calculating the test statistic. Assuming H_ω is true and that the error variance of individual observations is constant, the LR test statistic calculated using method (a) will be based on more observations than the LR test statistic calculated using method (d), and hence could be expected to better follow the X^2_r distribution. However, method (d) may be modified so that there are several dependent variable averages and weights at each value of the independent variable (see the section comparing methods (a) and (d)), and the number of observations maintained above the required level. A similar technique can be applied to method (c).

The problem of constructing LR tests thus reduces to one of finding LS estimates for a number of different probability models. These models are generated by placing appropriate linear constraints on the general model Ω, depending on the hypothesis being tested. For the single sample problem, linear constraints take the form of fixing any or all of the parameters (l_∞, K, t_0) to their hypothesized values. In this case, the degrees of freedom of X^2_r is equal to the number of parameters fixed. For the multisample problem, linear constraints take the form of fitting von Bertalanffy curves so that any or all of the parameters are equal in any or all of the I populations. In this case, the degrees of freedom of X^2_r is equal to the number of linear equations needed to specify the particular constraints. For example, $I-1$ linear equations are needed to specify equality of any parameter over I populations.

AN EXAMPLE

As an example illustrating some of the methods that have been presented, growth data (Table 1) for Pacific hake, *Merluccius productus*, from Dark (1975), was analyzed using method (b). The reader can test his understanding of methods, as well as the correctness of his computer programs, by duplicating this analysis.

A first step in nonlinear LS analysis is the selection of a general purpose iterative nonlinear LS computer program. Such programs take initial estimates and attempt to find LS estimates. For the present analysis, BMDO7R of the BMD biomedical computer programs (Dixon 1976) was used. This choice was dictated by program availability.

TABLE 1.—Average length at various ages for male and female Pacific hake taken off California, Oregon, and Washington during 1965-69 (adopted from Dark 1975).

Age (years)	Female		Male	
	Sample size	Mean length (cm)	Sample size	Mean length (cm)
1.0	385	15.40	385	15.40
2.0	36	26.03	28	26.93
3.3	17	41.18	13	42.23
4.3	135	46.20	83	44.59
5.3	750	48.23	628	47.63
6.3	1,073	50.26	1,134	49.67
7.3	1,459	51.82	1,761	50.87
8.3	626	54.27	432	52.30
9.3	199	56.98	93	54.77
10.3	97	58.93	21	56.43
11.3	44	59.00	8	55.88
12.3	11	60.91	—	—
13.3	6	61.83	—	—

Suitable programs are also available in BMDP (Dixon 1977), SPSS (Nie et al. 1975), and from a number of other sources.

Inital values were obtained from Ford-Walford plots (Ricker 1975) which provided estimates $\bar{l}_\infty$ and $\bar{K}$; and from the weighted average

$$\tilde{t}_0 = \frac{\sum_i [\log(1-\bar{l}_i/\bar{l}_\infty)/\bar{K} + t_i]\,(\bar{l}_\infty - \bar{l}_i)}{\sum_i (\bar{l}_\infty - \bar{l}_i)}$$

where $\bar{l}_i$ is the average length at age t_i. For these initial calculations, it was convenient to round ages to whole years. This disallows direct comparisons of Ford-Walford and LS estimates. Besides initial estimates, BMDO7R also requires a FORTRAN subroutine (provided in the Appendix) which evaluates $\mu(t_u)$ and its partial derivatives.

Table 2 contains the initial Ford-Walford estimates $(\bar{l}_\infty, \bar{K}, \tilde{t}_0)$ and the final LS estimates $(\hat{l}_\infty, \hat{K}, \hat{t}_0)$ obtained from BMDO7R. LS fits of growth curves are graphed in Figure 1.

From Figure 1 there appears to be a difference in l_∞ between sexes. As a further examination of this difference, cross sections of the approximate 95% confidence regions around $(\hat{l}_\infty, \hat{K})$, generated by conditioning on $\hat{t}_0$, were graphed (Figure 2) using

TABLE 2.—Least squares (LS) estimates of von Bertalanffy parameters for male and female Pacific hake, based on data in Table 1.

Item	l_∞	K	t_0
Male:			
Ford-Walford initial estimates	55.63	0.43	0.35
LS estimates	55.98	0.386	0.171
Standard deviation of LS estimates	1.083	0.039	0.142
Female:			
Ford-Walford initial estimates	60.60	0.35	0.32
LS estimates	61.23	0.296	−0.057
Standard deviation of LS estimates	1.214	0.029	0.175

methods previously described. These regions not only show a difference in l_∞ between sexes, but also indicate a difference in K.

As a final step in this analysis, LR tests for equality of von Bertalanffy parameters between males (population 1) and females (population 2) were performed. It was necessary to fit data to five models corresponding to hypotheses of interest (Table 3).

The difficulty of fitting these models depends somewhat on the nonlinear LS program used. If derivative-free programs are available, the user will be saved the complex task of specifying derivatives. If programs allow for constraints, only the model Ω need be specified. Nonlinear LS programs available in BMDP have these features.

For BMDO7R, the Appendix provides FORTRAN subroutines which evaluate $\mu(t_u)$ and its

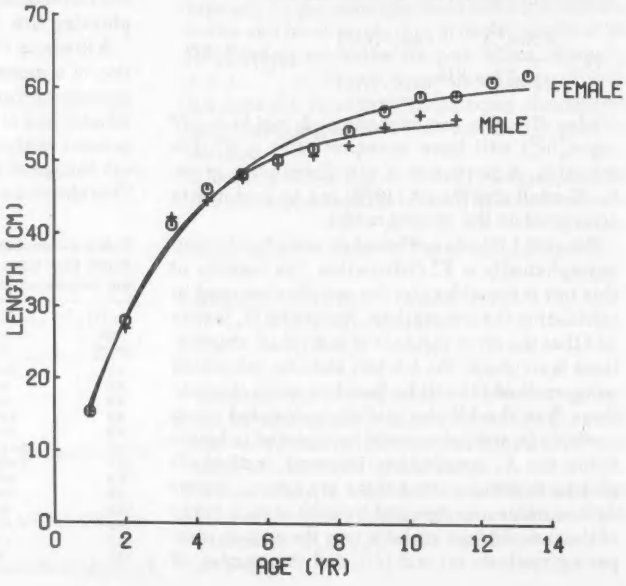

FIGURE 1.—Plots of average length at each age (from Table 1), for male and female Pacific hake, with graphs of estimated von Bertalanffy curves (from Table 2).

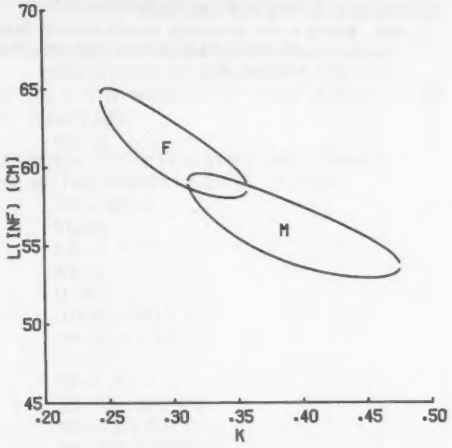

FIGURE 2.—Cross sections of approximate 95% confidence regions around least squares estimates ($\hat{l}_\infty, \hat{K}$), generated by conditioning on $\hat{t}_0$ (see text), for male (M) and female (F) Pacific hake. Letters M and F are centered on least squares estimates.

partial derivatives for the five models. These subroutines are general in the sense that they allow comparisons of any number of populations. Probably these subroutines are compatible with the requirements of BMDP3R, but this program was not readily available for a test. Also, minor modifications may be necessary to comply with requirements of particular computer systems.

Results of LR tests (Table 3) indicate there is a significant difference ($\alpha = 0.002$) in l_∞ between sexes, a borderline significant difference ($\alpha = 0.05$) in K, but no significant difference in t_0.

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TABLE 3.—Likelihood ratio tests comparing von Bertalanffy parameter estimates for male (1) and female (2) Pacific hake, based on data in Table 1 ($N = 24$ observations).

Hypothesis	Linear constraints	Equivalent model	$\hat{l}_{\infty 1}$	$\hat{l}_{\infty 2}$	$\hat{K}_1$	$\hat{K}_2$	$\hat{t}_{01}$	$\hat{t}_{02}$	Residual sum of squares ($N\hat{\sigma}^2$)	$\hat{X}_r^2 = -N \log (\hat{\sigma}_\Omega^2/\hat{\sigma}_\omega^2)$	df (r)	$P[X_r^2 > \hat{X}_r^2]$
H_Ω	none	$l_{ij} = l_{\infty i}(1-\exp(-K_i(t_{ij}-t_{0i})))$	55.98	61.23	0.386	0.296	0.171	−0.057	48.22			
$H_{\omega 1}$	$l_{\infty 1} = l_{\infty 2}$	$l_{ij} = l_\infty(1-\exp(-K_i(t_{ij}-t_{0i})))$	59.40	59.40	0.297	0.337	−0.111	0.087	71.60	9.49	1 ($l-1$)	0.002
$H_{\omega 2}$	$K_1 = K_2$	$l_{ij} = l_{\infty i}(1-\exp(-K(t_{ij}-t_{0i})))$	57.44	60.14	0.330	0.330	−0.021	0.095	56.34	3.74	1 ($l-1$)	0.053
$H_{\omega 3}$	$t_{01} = t_{02}$	$l_{ij} = l_{\infty i}(1-\exp(-K_i(t_{ij}-t_0)))$	56.45	60.77	0.361	0.313	0.057	0.057	50.76	1.23	1 ($l-1$)	0.267
$H_{\omega 4}$	$l_{\infty 1} = l_{\infty 2}$ $K_1 = K_2$ $t_{01} = t_{02}$	$l_{ij} = l_\infty(1-\exp(-K(t_{ij}-t_0)))$	59.29	59.29	0.320	0.320	0.010	0.010	79.76	12.08	3 $3(l-1)$	0.007

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APPENDIX

This appendix contains FORTRAN subroutines required by BMDO7R to fit models corresponding to the five hypotheses in Table 3. These subroutines evaluate $\mu(t_{ij})$ and its partial derivatives. To use these subroutines, the following three instructions need to be understood.

1. The variable NG must be set equal to the number of populations to be compared.

2. The first NG variables of the data input must be "design variables," followed by age. That is, the first NG variables for observation l_{ij} must consist of NG-1 zeros and a single one, the one occurring in the ith position; followed by age (t_{ij}). Next comes length and statistical weights (if weighting is used).

3. The parameters to be estimated are referenced in the order all l_∞'s first, all K's second, and all t_0's last. Relative positions of l_∞'s, K's, and t_0's amongst themselves are simply the order of population number. It should be noted that the number of parameters fitted under the five hypotheses of Table 3 are H_Ω: $3\times NG$; $H_{\omega 1}$,$H_{\omega 2}$,$H_{\omega 3}$: $(2\times NG)+1$; $H_{\omega 4}$: 3.

I. Subroutine FUN for hypothesis Ω.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS Ω:
C NG DIFFERENT GROWTH CURVES
      IND=NG+1
      XL=0.
      XK=0.
      XT=0.
      II=NG
      III=NG+NG
      DO 10 I=1,NG
      II=II+1
      III=III+1
      XL=XL+X(I)*P(I)
      XK=XK+X(I)*P(II)
      XT=XT+X(I)*P(III)
10    CONTINUE
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      II=NG
      III=NG+NG
      DO 20 I=1,NG
      II=II+1
      III=III+1
      D(I)=0.
      D(II)=0.
      D(III)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(I)=1.-XX
      D(II)=XL*XX*(X(IND)-XT)
      D(III)=-XL*XX*XK
20    CONTINUE
      RETURN
      END
```

II. Subroutine FUN for hypothesis ω1.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω1: l∞'S
C EQUAL
      IND=NG+1
      XK=0.
      XT=0.
      II=1
      III=1+NG
      DO 10 I=1, NG
      II=II+1
      III=III+1
      XK=XK+X(I)*P(II)
      XT=XT+X(I)*P(III)
10    CONTINUE
      XL=P(1)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      II=1
      III=1+NG
      DO 20 I=1,NG
      II=II+1
      III=III+1
      D(II)=0.
      D(III)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(II)=XL*XX*(X(IND)-XT
      D(III)=-XL*XX*XK
20    CONTINUE
      D(1)=1.-XX
      RETURN
      END
```

III. Subroutine FUN for hypothesis ω2.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω2: K'S
C EQUAL
      IND=NG+1
      INDX=NG+1
      XL=0.
      XT=0.
      III=NG+1
      DO 10 I=1,NG
      III=III+1
      XL=XL+X(I)*P(I)
      XT=XT+X(I)*P(III)
10    CONTINUE
      XK=P(INDX)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      III=NG+1
      DO 20 I=1,NG
      III=III+1
      D(I)=0.
      D(III)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(I)=1.-XX
      D(III)=-XL*XX*XK
20    CONTINUE
      D(INDX)=XL*XX*(X(IND)-XT)
      RETURN
      END
```

IV. Subroutine FUN for hypothesis ω3.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω3: t0'S
C EQUAL
      IND=NG+1
      INDX=NG+NG+1
      XL=0.
      XK=0.
      II=NG
      DO 10 I=1,NG
      II=II+1
      XL=XL+X(I)*P(I)
      XK=XK+X(I)*P(II)
10    CONTINUE
      XT=P(INDX)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      II=NG
      DO 20 I=1,NG
      II=II+1
      D(I)=0.
      D(II)=0.
      IF(X(I).EQ.0.) GO TO 20
      D(I)=1.-XX
      D(II)=XL*XX*(X(IND)-XT)
20    CONTINUE
      D(INDX)=-XL*XX*XK
      RETURN
      END
```

V. Subroutine FUN for hypothesis ω4.

```
      SUBROUTINE FUN(F,D,P,X)
      DIMENSION D(1),P(1),X(1)
C NG IS THE NUMBER OF POPULATIONS TO BE
C COMPARED
      NG=2
C SUBROUTINE FUN FOR HYPOTHESIS ω4: ALL
C CURVES IDENTICAL
      IND=NG+1
      XL=P(1)
      XK=P(2)
      XT=P(3)
      XX=EXP(-XK*(X(IND)-XT))
      F=XL*(1.-XX)
      D(1)=1.-XX
      D(2)=XL*XX*(X(IND)-XT)
      D(3)=-XL*XX*XK
      RETURN
      END
```

VERTICAL DISTRIBUTION AND DEVELOPMENT OF LARVAL FISHES IN THE NORTH PACIFIC CENTRAL GYRE DURING SUMMER

VALERIE J. LOEB[1]

ABSTRACT

Abundance data are presented on the mesopelagic fish larvae taken in 60 opening/closing bongo net samples from the North Pacific central gyre in late summer. Vertical abundance and size-depth distributions are described for 43 species of gonostomatids and myctophids and two sternoptychid genera. Developmental stages at which these fishes leave the surface layers (either moving deeper or beginning extensive vertical migration) are estimated from sizes of captured larvae.

Over 96% of the estimated larval water column abundance occurred within the upper 100 m. Maximum abundance and diversity were at 25-50 m, possibly related to the bottom of the seasonal mixed layer. Most of the abundant species had distinct depths of maximum abundance within one of the 25 m depth intervals sampled and demonstrated changes in size composition with depth. Different larval distributional patterns were found within and between the Gonostomatidae, Sternoptychidae, and Myctophidae. Larvae of the two myctophid subfamilies had significantly different overall vertical distribution patterns; Myctophinae larvae were more deeply distributed than Lampanyctinae larvae. The myctophids exhibited two patterns of ontogenetic migration: one group of species remains in the surface layers until transformation; the other leaves the surface layers in early stages of photophore development.

Mesopelagic fish species dominate the fish fauna in oceanic regimes, both in terms of numbers of species and numbers of individuals. The adults are important components of oceanic communities. The vertically migrating and more active species are known predators upon other nekton and upon zooplankton (Pearcy and Laurs 1966; Legand and Rivaton 1969; Merrett and Roe 1974). We know much about the depth distributions and diurnal migrations of adult fish species; comparatively little is known of the vertical distributions of their early life stages.

The larvae of most mesopelagic fish species are found within the upper several hundred meters of the water column (Ahlstrom 1969) where they are part of the zooplankton. This larval fish fraction of zooplankton assemblages is called the ichthyoplankton. Ahlstrom's (1959) study of vertical distributions of larval fishes in the California Current included some mesopelagic species. He found that the majority of the species occurred within the mixed layer and upper thermocline and that each species had a characteristic depth distribution; these depth distributions, however, varied with the highly variable (10-90 m) mixed layer depth.

Larval fishes grow and develop within the upper levels until some point of development when the individuals leave the plankton and adopt juvenile-adult roles. Changes in depth distribution with larval development and the stage(s) of development at which the young leave the upper levels and either descend to juvenile depths or begin extensive vertical migrations have not previously been reported.

The North Pacific central gyre is an excellent area in which to examine the vertical distribution of ichthyoplankton. Physically the upper several hundred meters are horizontally monotonous and vertically well stratified (McGowan and Hayward 1978; Gregg et al. 1973). In contrast to the California Current, the summertime mixed layer depth (ca. 40 m) is quite constant. The ichthyoplankton is composed of a diverse and rather equitably distributed assemblage of mesopelagic fish species. Overall species composition and relative abundance relations of larvae taken in integrating 0-300 m Isaacs-Kidd plankton trawl samples are similar from tow to tow within and between summers (Loeb 1979b); repeated patterns of species composition and abundance relations also occur in replicated bongo samples taken within the same depth interval (Loeb 1979a).

In this study I present catch information on a large number of larval fish species taken in 60

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opening/closing bongo net samples during a stratified sampling program in the North Pacific central gyre (Scripps Institution of Oceanography 1974). I describe the vertical abundance and size-depth distributions of the more abundant families (Gonostomatidae, Sternoptychidae, and Myctophidae) and species. I also present estimates of the predescent stages of development of species for which there are sufficient catch data.

METHODS

All depth stratified samples were obtained during Climax I expedition (19-28 September 1968; Scripps Institution of Oceanography 1974) near lat. 28° N, long. 155° W. The physical, chemical, and biological properties at this locale have been shown to be stable over large time and space scales (McGowan and Walker in press) and are expected to be representative of the central gyre (Scripps Institution of Oceanography 1974). During this cruise, round-the-clock sampling was done with opening/closing bongo nets (Scripps Institution of Oceanography 1966) between a set of parachute drogues placed at 10 m depth about 10 km apart. The drogues traveled 346 km during the 10 days of sampling. The main depth intervals sampled were: 0-25 m, 25-50 m, 50-75 m, 75-100 m, 100-350 m, and 350-600 m; other intervals were also sampled. Paired 505 μm nets on the 70 cm diameter frames each had a mouth area of 0.396 m^2. They were opened at the bottom of the desired depth range and fished obliquely upward, closing near the top of the range. Maximum tow depths were determined by Benthos[2] depth-telemetering pinger and/or wire angle. The nets were closed automatically by a calibrated flowmeter after 400 m^3 of water had been filtered per net. Ship speed was nominally 2.5 kn.

All fishes were sorted from 60 samples representing 38 separate tows (one sample equals the catch from one of the paired nets). Samples included: ten each from 0-25 m, 25-50 m, 50-75 m, and 75-100 m; six from 100-225 m; six from 100-350 m; and eight from 350-600 m (Table 1).

To reduce biases due to net avoidance by larger individuals and more agile species (Bridger 1956; Ahlstrom 1959) most analyses were of "night" samples (taken between 2000 and 0600 local time). To provide enough replicate samples to allow statistical analyses of strata deeper than 50 m, I found it necessary to include 11 "day" samples; these were selected from tows taken as close to dawn or dusk as possible. As a result, this study does not include aspects of diurnal changes in depth distributions. Ahlstrom (1959) and Badcock and Merrett (1976) showed that the larvae of some midwater fishes (size or stage of development unreported) do undergo limited diurnal migrations.

I identified all fishes caught to the lowest taxon possible. These were categorized to stage of development (i.e., larval, metamorphic, postmetamorphic or juvenile, adult), enumerated and measured to the nearest 0.1 mm standard length (SL) (notochord length was measured for preflexion larvae). The data presented in this paper (unless otherwise noted) are based on larval to early

TABLE 1.—Opening/closing bongo net samples used for larval fish depth distribution analyses. Samples taken near lat. 28° N, long. 155° W in the North Pacific central gyre during September 1968. L and R designate left or right sample from paired net assembly. Mean and standard deviations of temperature at upper (T_U) and lower (T_L) limits of each interval based on 10 day and 7 night 0-500 m STD lowerings.

Depth interval (m)	Date (Sept. 1968)	Time	Net	Temperature (C°) T_U	Temperature (C°) T_L
0-25	21	0250-0325	L & R	27.10±0.20	26.85±0.24
	22	0408-0445	L & R		
	23	0247-0330	R		
	26	2118-2137	L & R		
	27	0040-0103	R		
	27	0341-0404	L & R		
25-50	21	0250-0325	L & R	26.85±0.24	24.94±1.01
	22	0408-0445	L & R		
	23	0247-0330	L		
	24	0507-0540	L & R		
	26	2118-2137	R		
	27	0040-0103	R		
	27	0341-0404	L		
50-75	21	0250-0325	R	24.94±1.01	21.45±0.31
	22	0408-0445	R		
	26	1859-1922	L & R		
	26	2206-2230	L & R		
	27	0126-0156	L & R		
	27	0449-0510	L		
	27	0804-0838	R		
75-100	21	0250-0325	R	21.45±0.31	20.51±0.21
	22	0408-0445	R		
	24	0413-0500	L		
	26	1859-1922	L & R		
	26	2208-2230	L & R		
	27	0126-0156	R		
	27	0449-0510	L & R		
100-225	21	0529-0600	L	20.51±0.21	15.28±0.30
	21	1638-1656	L & R		
	22	0214-0234	L & R		
	24	0046-0111	L		
100-350	26	2010-2033	L & R	20.51±0.21	10.52±0.27
	27	0237-0255	L & R		
	27	0606-0633	L & R		
350-600	26	2010-2033	L & R	10.52±0.27	Not available
	26	2328-2351	L & R		
	27	0237-0255	L & R		
	27	0606-0633	L & R		

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

metamorphic stages only; juvenile and adult information is provided separately. I was able to identify most of the abundant larvae to species. Some of the larvae, however, could not be identified with certainty. For these I assigned "probable" and "possible" species names. These designations were based on the accumulation of enough larvae to establish developmental links to known adult species (Loeb 1979b, >29,000 larval identifications) and a list of adult central gyre mesopelagic fish species and their relative abundances (Barnett 1975).

For analyses of abundance distributions with depth, the larval fish catches from each sample were converted to numbers per 1,000 m^3. These were averaged for each depth interval and then summed to provide estimated water column abundance. Individual species distributions are expressed as percent of their estimated water column abundance caught within each of the main depth intervals sampled. The 100-225 m catches were used in calculations only if they contained species not present in 100-350 m or 350-600 m samples. The 100-225 m and 100-350 m samples were compared to assess whether larval abundance was concentrated in the upper portion of the larger depth range.

Significance of differences in size composition with depth were determined, where sample sizes permitted, using the Kolmogorov-Smirnov test (Conover 1971) on cumulative size-frequency distributions of 0.5 mm (SL) categories of the total larvae taken (all samples combined) within each depth interval. A one-tailed probability of the maximum difference between cumulative size-frequency distributions in two depth strata ≤ 0.05 was deemed "significant." Rejection of the null hypothesis of no difference indicates that one of the size distributions being compared is significantly larger than the other. The results of these tests are in no case altered by the exclusion of larvae from the "day" samples in their calculation.

Descriptions of the developmental stages of myctophid larvae in the plankton include additional information obtained from six other central gyre cruises in the vicinity of lat. 28° N, long. 155° W. These cruises utilized Isaacs-Kidd plankton trawls (IKPT) fished obliquely from the surface to about 300 m (Loeb 1979b). Those data (24,500 identified larvae) provide a broader range of larval sizes and developmental stages, and development from early larvae to metamorphosis (transformation) has been traced for many species. I used this information as an aid for estimating levels of development reached while larvae are still in the upper water column, prior to descent to deeper juvenile-adult depths.

RESULTS

I identified a total of 5,448 larvae (Table 2). These included 94 generic and species identifications from 36 families, and one ordinal grouping. Three families (Gonostomatidae, Sternoptychidae, and Myctophidae) together contributed 91% of the individuals and 50% of the species.

Larvae were taken throughout the 600 m depth range (Figure 1a); however, over 97% of the estimated water column abundance was in the upper 100 m. Only 13 of the 95 kinds of larvae appeared to have maximum abundance below 100 m. Maximum larval abundance (and diversity, or number of species) occurred within the 25-50 m interval (Figure 1a); the bottom of the summer mixed layer (ca. 40 m) is within this interval (Figure 1b). Total larval abundance (Figure 1a) as well as individual species abundances were highly variable from tow to tow within each interval. Despite this variability, most species demonstrated a definite peak of abundance (generally >60% of their estimated water column abundance) and

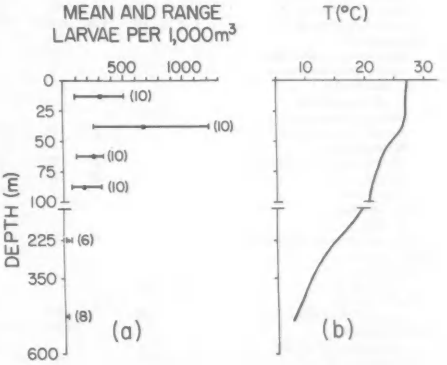

FIGURE 1.—Vertical distribution of ichthyoplankton in relation to late summer thermal structure in the North Pacific central gyre. (a) Mean and range of total numbers of larvae per 1,000 m^3 caught in replicate samples within each depth interval (bracketed values are numbers of replicate samples). (b) Temperature profile of upper water column during Climax I, based on average values from 10 day and 7 night STD lowerings.

TABLE 2.—Total numbers of individuals (N) and rank of numerical abundance (R) of larval fish species caught (n samples combined) within each of seven depth intervals in the North Pacific central gyre during late summer.

Species	0-25 m n =10		25-50 m n = 10		50-75 m n= 10		75-100 m n = 10		100-225 m n = 6		100-350 m n = 6		350-600 m n = 8		Total	
	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N	R
Gonostomatidae:																
Cyclothone alba	580	(1)	887	(1)	171	(1)	17	(12)	3	(13½)					1,458	(1)
C. sp. A (prob. pseudopallida)	43	(5)	9	(26½)	2	(37)									60	(19)
C. atraria	1	(36)													1	(100)
C. spp.	76	(4)	78	(10)	28	(11)	4	(27½)			2	(11)	5	(1)	193	(7)
Diplophos taenia	13	(11)	1	(54)											14	(42½)
Gonostoma atlanticum							30	(6)	9	(3)	2	(11)			41	(29)
G. elongatum							10	(14)	2	(18½)	2	(11)			14	(42½)
Ichthyococcus ovatus							7	(18)	5	(8½)					12	(45)
Margrethia obtusirostra									4	(10½)					4	(73½)
Valenciennellus tripunctulatus									6	(6)	3	(7½)			9	(52)
Vinciguerria nimbaria	6	(18)	376	(2)	99	(2)	25	(8)	7	(4)	1	(19)			514	(2)
V. poweriae					2	(37)	60	(2)	5	(8½)	4	(5)			71	(16)
V. spp.	3	(25½)	90	(9)	61	(5)	34	(5)	3	(13½)	13	(1)			204	(6)
Woodsia sp.							4	(27½)	1	(26½)					5	(67)
Sternoptychidae:																
Argyropelecus spp.											1	(19)	4	(2)	5	(67)
Sternoptyx diaphana									14	(1)	5	(3)			19	(38½)
S. pseudobscura							1	(46½)	4	(10½)			1	(4)	6	(61)
S. spp.									6	(6)	4	(5)			10	(50)
Myctophidae:																
Lampanyctinae:																
Bolinichthys distofax			27	(17)											27	(30)
B. longipes	177	(2)	47	(11)	1	(46)									225	(5)
B. spp.	30	(6)	21	(21)											51	(23½)
Ceratoscopelus warmingi	15	(8)	235	(3)	47	(6)	2	(35)	1	(26½)					300	(3)
Diaphus anderseni	84	(3)	40	(13)	5	(25)					1	(19)			130	(12)
D. "slender B" (D. mollis B?)			2	(44½)	7	(21)	2	(35)							11	(48)
D. "slender C" (D. mollis A?)	12	(12)	95	(8)	9	(17½)	2	(35)					1	(4)	119	(13)
D. brachycephalus	6	(18)	30	(16)	14	(15)	1	(46½)							51	(23½)
D. "slender spp."	10	(14½)			6	(23)	2	(35)	1	(26½)					19	(38½)
D. elucens (= perspiciliatus)	18	(7)	164	(4)	46	(7)	2	(35)							230	(4)
D. roibolini (= phillipsi)	2	(28½)	97	(7)	27	(12)	5	(24)	2	(18½)	1	(19)			134	(10)
D. "stubby C" (D. schmidti?)	5	(21)	11	(24½)	7	(21)									23	(34½)
D. "stubby spp."							1	(46½)							1	(100)
Lampadena anomala	5	(21)	3	(39)											8	(55½)
L. luminosa	11	(13)	11	(24½)			1	(46½)							23	(34½)
Lampanyctus "big snout"			16	(23)	2	(37)									18	(40)
L. "lacks pectorals"			4	(33½)	33	(9)	7	(18)	1	(26½)					45	(26)
L. nobilis	1	(38)	23	(19)	2	(37)									26	(31)
L. steinbecki	3	(25½)	123	(6)	12	(16)									138	(9)
L. spp.			7	(29½)									1	(4)	8	(55½)
Loblanchia gemellari					29	(10)	26	(7)	2	(18½)					57	(21)
Notolychnus valdiviae					2	(37)	40	(4)			2	(11)			44	(27)
Triphoturus nigrescens	6	(18)	128	(5)	8	(19)	4	(27½)							146	(8)
Myctophinae:																
Benthosema suborbitale							48	(3)	11	(2)	6	(2)			65	(17½)
Centrobranchus andreae							1	(46½)							1	(100)
C. brevirostris							1	(46½)							1	(100)
C. choerocephalus							5	(24)							5	(67)
Diogenichthys atlanticus							8	(15½)	2	(18½)	2	(11)			12	(45)
Hygophum proximum			26	(18)	95	(3)	11	(13)							132	(11)
H. reinhardti					45	(8)	19	(11)	1	(26½)					65	(17½)
Myctophum brachygnathum			17	(22)	3	(30½)	1	(46½)							21	(36½)
M. lychnobium			32	(15)	18	(13)	8	(15½)							58	(20)
M. nitidulum					1	(46)	6	(21)							7	(58½)
M. selenops					5	(25)									5	(67)
M. spp.									2	(18½)	1	(19)			3	(78½)
Symbolophorus evermanni			9	(26½)	76	(4)	22	(9)	1	(26½)					108	(14)
Other Larvae:																
Congridae:																
Ariosoma sp.	1	(38)													1	(100)
Nemichthyidae:																
Nemichthys scolopaceus	1	(38)	1	(54)											2	(84½)
Bathylagidae:											1	(19)			1	(100)
Bathylagus bericoides																
B. longirostris									3	(13½)	1	(19)			4	(72½)
Stomiatoid fishes[1]	2	(28½)	22	(20)	16	(14)	2	(35)							42	(28)
Idiacanthidae:																
Idiacanthus fasciola					1	(46)	7	(18)							8	(55½)
Paralepididae:																
Type A (prob. *Lestidium nudum*)	2	(28½)	1	(54)	2	(37)									5	(67)
Type B (like *L. interpacificum*)	7	(16)	7	(29½)	2	(37)									16	(41)
Type D (prob. Gen. nov. sp. nov.)					4	(28)									4	(73½)
Paralepis atlantica									2	(18½)					2	(84½)
Stemonosudis macrura	1	(38)	4	(33½)	4	(28)									9	(52)

TABLE 2.—Continued.

Species	0-25 m $n = 10$		25-50 m $n = 10$		50-75 m $n = 10$		75-100 m $n = 10$		100-225 m $n = 6$		100-350 m $n = 6$		350-600 m $n = 8$		Total	
	N	R	N	R	N	R	N	R	N	R	N	R	N	R	N	R
Sudis atrox			2	(44½)	2	(37)	2	(35)							6	(61)
Uncisudis advena			1	(54)	2	(37)	5	(24)							8	(55½)
Unidentified Paralepidids			1	(54)	2	(37)									3	(78½)
Alepisauridae:																
Alepisaurus ferox					3	(30½)	2	(35)							5	(67)
Evermannellidae:																
Evermannella indica			4	(33½)	1	(46)									5	(67)
Odontostomops normalops	2	(28½)	44	(12)	7	(21)									53	(22)
Unidentified evermannellids			2	(44½)											2	(84½)
Scopelarchidae:																
Scopelarchus spp.							4	(27½)	3	(13½)	4	(5)			11	(48)
Notosudidae:																
Ahliesaurus brevis	10	(14½)	1	(54)											11	(48)
Scopelosaurus smithi	14	(9½)	8	(28)			3	(30)							25	(32)
Neoscopelidae:																
Scopelengys sp. (prob. *clarkei*)			2	(44½)											2	(84½)
Giganturidae:																
Bathyleptus lisae			1	(54)											1	(100)
Melanocetidae:																
Melanocetus johnsoni	4	(23½)			1	(46)									5	(67)
M. sp.	1	(38)													1	(100)
Oneirodidae:																
Dolopichthys longicornis			3	(39)											3	(78½)
Oneirodid A (poss. *Lasiognathus* sp.)	1	(38)													1	(100)
Unidentified oneirodids			3	(39)											3	(78½)
Gigantactinidae:																
Gigantactis sp. (prob. *vanhoeffeni*)	1	(38)	4	(33½)											5	
Ceratiidae:																
Ceratias holboelli			1	(54)											1	(100)
Cryptopsaras couesi	5	(21)	4	(33½)											9	(52)
Caulophrynidae:																
Caulophryne jordani					1	(46)									1	(100)
Unidentified ceratioids	4	(23½)	3	(39)											7	(58½)
Bregmacerotidae:																
Bregmaceros spp.					5	(25)	76	(1)	6	(6)	1	(19)			88	(15)
Ophidiidae:																
Brotulid (poss. *Lamprogrammus niger*)			1	(54)											1	(100)
Macrouridae:																
Mesobius berryi											1	(19)			1	(100)
Exocoetidae:																
Unidentified exocoetids			3	(39)	1	(46)									4	(73½)
Melamphaeidae:																
Melamphaes simus							6	(21)							6	(61)
M. sp. A (prtb. *indicus*)			1	(54)			1	(46½)							2	(84½)
M. spp.							1	(46½)							1	(100)
Scopeloberyx spp.							20	(10)	1	(26½)	3	(7½)			24	(33)
Scopelogadus mizolepis mizolepis							2	(35)							2	(84½)
Unidentified melamphaeids							1	(46½)							1	(100)
Anoplogasteridae:																
Anoplogaster cornuta			1	(54)											1	(100)
Zeidae:																
Unidentified zeid									1	(26½)					1	(100)
Trachipteridae:																
Trachipterus sp.			1	(54)											1	(100)
Stylephoridae:																
Stylephorus chordatus											1	(19)			1	(100)
Apogonidae:																
Howella sp.	1	(38)	39	(14)	9	(17½)									49	(25)
Bramidae:																
Brama japonica	1	(38)	2	(44½)											3	(78½)
Coryphaenidae:																
Coryphaena sp. (prob. *equiselis*)	1	(38)													1	(100)
Chiasmodontidae:																
Unidentified chiasmodontid	1	(38)													1	(100)
Gempylidae:																
Gempylus serpens	14	(9½)	4	(33½)	2	(37)	1	(46½)							21	(36½)
Trichiuridae:																
Diplospinus multistriatus			1	(54)	4	(28)	6	(21)	1	(26½)					12	(45)
Type A (poss. *Aphanopus carbo*)									1	(26½)					1	(100)
Unidentified trichiurid							1	(46½)							1	(100)
Scombridae:																
Acanthocybium sp.	1	(38)													1	(100)
Katsuwonus pelamis	1	(38)	2	(44½)											3	(78½)
Nomeidae:																
Cubiceps caeruleus	1	(38)													1	(100)

TABLE 2.—Continued.

Species	0-25 m n = 10 N	R	25-50 m n = 10 N	R	50-75 m n = 10 N	R	75-100 m n = 10 N	R	100-225 m n = 6 N	R	100-350 m n = 6 N	R	350-600 m n = 8 N	R	Total N	R
Total larvae identified	1,190		2,583		932		557		111		63		12		5,448	
Unidentified larvae	143		347		89		106		22		11		8		726	
Total larvae	1,333		2,930		1,021		663		133		74		20		6,174	
Number of rankings	41		60		49		50		31		24		7		112	

[1]Stomiatoid fishes include Astronesthidae, Malacosteidae, Melanostomiatidae, and Stomiatidae.

frequency of occurrence within one of the 25 m depth intervals. For many of the more abundant species, the catches in replicate tows within this interval were significantly greater (Mann-Whitney U test, $P \leq 0.05$) than those in adjacent intervals (Table 3).

TABLE 3.—Gonostomatidae, Sternoptychidae, and Myctophidae: Total estimated water column abundance of larval species during late summer in the North Pacific central gyre, based on summation of mean estimated abundances (numbers/1,000 m[3]) from each depth

Species	Total no. per 1,000 m[3]	0-25 m F (10)	0-25 m %	0-25 m Median length (mm)	0-25 m Range (mm)	25-50 m F (10)	25-50 m %	25-50 m Median length (mm)	25-50 m Range (mm)	50-75 m F (10)	50-75 m %	50-75 m Median length (mm)	50-75 m Range (mm)
Gonostomatidae:													
Cyclothone alba	365.0	10	39.7	5.6	3.2-12.6	10	47.0	4.5	2.5-12.2	10	11.7	7.9	2.2-12.4
C. sp. A	15.0	9	[1]81.7	5.9	3.2-13.8	6	15.0	7.6	4.9-13.9	2	3.3	9.4	5.0-13.7
C. atraria	0.2	1	100.0	4.6									
Diplophos taenia	3.5	7	[1]92.9	11.0	5.2-26.8	1	7.1	12.6					
Gonostoma atlanticum	8.3												
G. elongatum	3.3												
Ichthyococcus ovatus	3.8												
Margrethia obtusirostra	1.7												
Valenciennellus tripunctulatus	1.2												
Vinciguerria nimbaria	127.0	5	1.2	9.0	6.8-11.9	10	[1]74.1	7.2	3.7-14.5	10	19.5	14.0	3.7-17.5
V. poweriae	17.2									2	2.9	8.8	7.2-10.3
Woodsia sp.	1.4												
Sternoptychidae:													
Argyropelecus spp.	1.7												
Sternoptyx spp.	4.3												
Myctophidae:													
Lampanyctinae:													
Bolinichthys distofax	6.8					5	100.0	5.7	3.2-8.8				
B. longipes	56.2	10	[1]78.7	4.6	3.1-8.4	8	20.9	5.1	3.4-8.2	1	0.4	8.7	
Ceratoscopelus warmingi	75.2	4	5.0	4.0	3.2-4.7	10	[1]78.2	5.0	2.7-7.7	10	15.6	6.3	4.8-8.3
Diaphus anderseni	32.7	10	[1]64.3	4.2	2.7-6.5	7	30.6	4.5	3.2-7.1	2	3.8	7.0	5.3-11.6
D. "slender B"	2.8					2	18.2	3.6	2.5-4.6	2	63.6	5.6	3.5-6.3
D. "slender C"	29.8	3	10.1	3.8	2.6-5.0	9	[1]79.7	4.5	2.3-6.5	4	7.6	4.9	4.5-6.3
D. brachycephalus	12.8	3	11.8	4.0	3.7-4.6	6	58.8	4.2	2.6-5.9	5	27.4	5.4	4.3-8.7
D. elucens	57.5	8	7.8	3.5	2.8-4.8	10	[1]71.3	4.0	2.6-8.7	6	20.0	5.5	2.6-8.6
D. rolfbolini	33.2	1	1.5	3.4	3.3-3.5	10	[1]73.1	4.0	2.7-6.6	8	20.4	4.7	2.9-7.7
D. "stubby C"	5.8	2	21.7	3.5	3.2-3.8	2	47.8	3.7	3.0-4.2	2	30.4	3.6	3.3-3.8
Lampadena anomala	2.0	5	62.5	5.1	3.4-5.8	3	37.5	3.7	2.9-6.2				
L. luminosa	5.8	4	47.8	5.0	3.7-5.9	4	47.8	6.8	3.4-8.6				
Lampanyctus "big snout"	4.5					7	[1]88.9	4.0	2.8-7.1	2	11.1	5.6	3.9-7.4
L. "lacks pectorals"	11.4					3	8.8	4.0	3.5-5.9	9	[1]72.2	4.4	2.6-6.2
L. nobilis	6.5	1	3.8	5.4		5	88.5	4.8	2.9-10.5	2	7.7	7.8	5.4-10.2
L. steinbecki	34.5	3	2.2	3.2	3.2-4.2	10	[1]89.1	3.4	2.1-5.5	4	8.7	4.4	2.9-6.9
Loblamichthys gemellari	14.6									8	49.7	4.4	2.8-5.8
Notolychnus valdiviae	11.3									2	4.4	4.0	3.1-10.5
Triphoturus nigrescens	36.5	4	4.1	5.0	2.3-7.4	10	[1]87.7	4.4	2.7-8.1	4	5.5	6.7	5.2-7.9
Myctophinae:													
Benthosema suborbitale	14.5												
Centrobranchus andreae	0.2												
C. brevirostris	0.2												
C. choerocephalus	1.2												
Diogenichthys atlanticus	2.8												
Hygophum proximum	33.0					9	19.7	3.8	2.8-5.9	10	[1]72.0	4.5	2.3-8.7
H. reinhardti	16.4									9	[1]68.5	6.5	3.8-9.4
Myctophum brachygnathum	5.2					6	81.0	2.9	2.3-4.1	2	14.3	3.9	2.5-4.8
M. lychnobium	14.5					7	55.2	3.7	2.8-5.8	5	31.0	3.6	2.5-4.6
M. nitidulum	1.8									1	14.3	3.9	
M. selenops	1.2									2	100	4.7	3.4-5.4
Symbolophorus evermanni	27.2					3	8.3	5.5	3.9-6.2	9	[1]69.9	4.5	2.8-5.6

[1]Designates abundances which, based on abundances within replicate tows, are significantly greater (Mann-Whitney U-test, $P \leq 0.05$) than in any other depth interval.
[2]Denotes use of 100-225 m instead of 100-350 m samples.

Gonostomatid and myctophid larvae made up most of the ichthyoplankton in the upper 100 m (Figure 2). The "other larvae" were a low, constant percent of the total from the surface to 75 m, but their percent contribution was markedly increased between 75 and 350 m. Below 350 m most of the larvae were sternoptychids and gonostomatids.

Family Gonostomatidae

The gonostomatids (8 genera, 12 species) composed 48% of the identified larvae. The family was an important fraction of the total larvae in all strata (Figure 3a); 97% of the estimated family abundance occurred above 100 m. Maximum abundance was at 25-50 m due to concentrations of the two most abundant species *Cyclothone alba*

interval; and frequency of occurrence (F) in (*n*) samples, percent of total estimated water column abundance, median length, and size range (mm standard length) within each depth interval.

Species	75-100 m F (10)	%	Median length (mm)	Range (mm)	100-350 m F (6)	%	Median length (mm)	Range (mm)	350-600 m F (8)	%	Median length (mm)
Gonostomatidae:											
Cyclothone alba	5	1.2	9.2	3.7-14.7	[2]2	0.3	4.1	3.8-4.7			
C. sp. A											
C. atraria											
Diplophos taenia											
Gonostoma atlanticum	7	90.0	6.1	2.7-16.3	1	10.0	6.5	2.7-12.9			
G. elongatum	5	75.1	5.4	3.7-12.2	2	24.9	6.5	4.3-8.2			
Ichthyococcus ovatus	3	45.7	8.0	5.8-13.2	[2]3	54.3	11.0	4.0-16.3			
Margrethia obtusirostra					[2]3	100	4.6	2.8-8.2			
Valenciennellus tripunctulatus					2	100	8.6	7.1-9.9			
Vinciguerria nimbaria	9	4.9	14.2	3.9-17.8	1	0.3	4.5	3.7-7.1			
V. poweriae	9	87.4	10.8	6.5-19.2	2	9.7	12.1	6.8-19.7			
Woodsia sp.	2	70.4	5.9	3.7-6.2	[2]1	29.6	3.2				
Sternoptychidae:											
Argyropelecus spp.					1	25.2			2	75.8	
Sternoptyx spp.	1	5.8			4	87.0			1	7.2	
Myctophidae:											
Lampanyctinae:											
Bolinichthys distofax											
B. longipes											
Ceratoscopelus warmingi	2	0.7	10.7	8.6-12.8	[2]1	0.5	11.8				
Diaphus anderseni					1	1.3	10.5				
D. "slender B"	2	18.2	8.8	6.2-10.0							
D. "slender C"	2	1.7	6.6	4.3-8.9					1	1.0	4.9
D. brachycephalus	1	2.0	6.1								
D. elucens	2	0.9	6.8	4.8-8.9							
D. rolfbolini	3	3.8	6.9	4.9-9.9	1	1.3	4.7	2.9-7.8			
D. "stubby C"											
Lampadena anomala											
L. luminosa	1	4.4	12.7								
Lampanyctus "big snout"											
L. "lacks pectorals"	4	15.3	5.7	3.2-6.8	[2]1	3.7	4.3				
L. nobilis											
L. steinbecki											
Lobianchia gemellari	9	44.6	3.8	3.2-7.9	[2]2	5.7	4.0	3.7-4.2			
Notolychnus valdiviae	8	[1]88.3	5.2	3.3-8.0	2	7.3	6.2	6.1-6.4			
Triphoturus nigrescens	2	2.7	7.6	6.2-11.8							
Myctophinae:											
Benthosema suborbitale	4	82.8	3.6	2.5-7.8	3	17.2	3.9	1.8-8.0			
Centrobranchus andreae	1	100	5.9								
C. brevirostris	1	100	5.3								
C. choerocephalus	3	100	6.2	3.4-7.1							
Diogenichthys atlanticus	4	70.7	4.9	4.3-5.8	2	29.3	4.2	3.8-4.6			
Hygophum proximum	5	8.3	5.5	2.2-10.8							
H. reinhardti	7	28.9	6.5	2.4-13.1	[2]1	2.6	4.6				
Myctophum brachygnathum	1	4.7	7.5								
M. lychnobium	3	13.8	3.6	2.2-4.2							
M. nitidulum	3	85.7	3.7	2.7-4.9							
M. selenops											
Symbolophorus evermanni	8	20.2	4.4	3.3-10.5	[2]1	1.6	4.7				

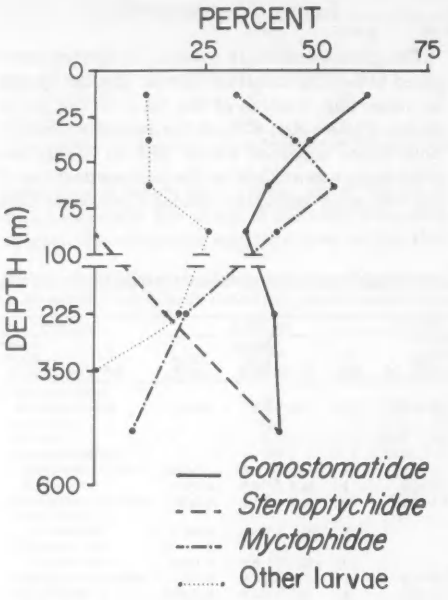

FIGURE 2.—Percent contribution of major families and "other larvae" to the total ichthyoplankton caught within each depth interval of the North Pacific central gyre during summer.

and *Vinciguerria nimbaria* (Figure 3b). Maximum diversity occurred at 75-225 m.

CYCLOTHONE SPP.—*Cyclothone alba* is a numerous larval fish species in the central gyre throughout the year, ranking second in abundance only to *Vinciguerria nimbaria* (Loeb 1979b). It was the most abundant species taken during this cruise (27% of all larvae), and was present in all samples from 0 to 75 m; below 75 m it was rare (Table 2). Eighty-seven percent of the estimated water column abundance was from the upper 50 m, with highest concentrations at 25-50 m (Figure 3b). Abundances in replicate tows within the 0-25 m and 25-50 m intervals were not significantly different from each other; they were, however, significantly greater (Mann-Whitney U test, $P < 0.01$) than those in deeper intervals.

A wide range of larval lengths was found within each depth interval from 0 to 75 m and the cumulative size-frequency curves differed significantly (Kolmogorov-Smirnov test, $P < 0.05$) between all three intervals (Figure 4). There was no simple

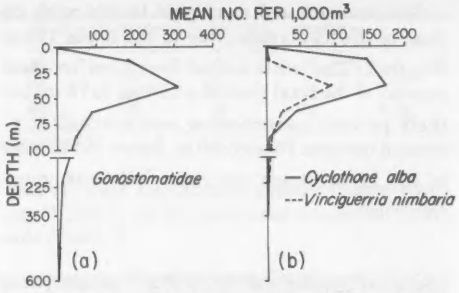

FIGURE 3.—Vertical distributions of larval gonostomatids in the North Pacific central gyre during summer. Concentrations of (a) gonostomatid larvae (12 species combined) and of (b) *Cyclothone alba* and *Vinciguerria nimbaria* larvae by depth interval.

increase in standard length with depth: smaller sizes dominated at 25-50 m, larger lengths at 50-75 m, and intermediate sizes at 0-25 m. Although median standard length was largest in the 75-100 m interval, the cumulative size-frequency curve was not significantly different from that at 50-75 m, possibly because of the paucity of larvae captured at 75-100 m. The three largest larvae present in 75-100 m samples (11.6-14.7 mm) were in the prometamorphic (white photophore) stage (Ahlstrom and Counts 1958) of development. Only three small larvae were caught between 100 and 350 m, and 57 metamorphosed individuals were caught at 350-600 m.

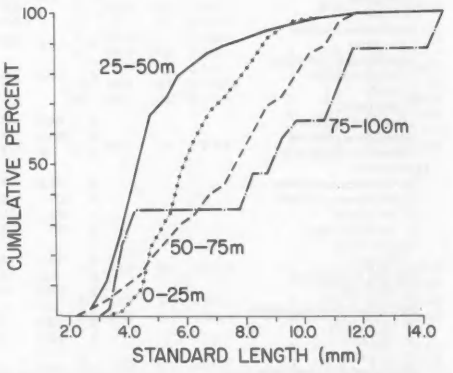

FIGURE 4.—Cumulative size-frequency curves for *Cyclothone alba* larvae by 25 m depth interval (10 samples per interval) within the upper 100 m of the North Pacific central gyre during summer.

Most of the smallest *C. alba* larvae apparently occur near the bottom of the mixed layer, and move first up and then downward with increasing size and development; the most advanced stage attained in 0-100 m is prometamorphic. A rapid descent may then occur, indicated by the near absence of any individuals in 100-225 m and 100-350 m samples. Photophore completion and metamorphosis probably occur at depths >350 m, in agreement with Ahlstrom's (1974) report that only the white photophore stage of *Cyclothone* spp. is found above 200 m, and that more advanced stages occur deeper in the water column.

Kobayashi (1973) gives a 300-1,000 m depth range for adult Pacific *C. alba*. He found that the individuals occurring in the range of maximum abundance (400-600 m) were smaller than those occurring shallower or deeper; intermediate-sized adults were shallower and largest adults were deeper. This size distribution of the adults parallels that found herein for the larvae, although shifted well downwards in the water column.

Cyclothone sp. A is probably the larval form of *C. pseudopallida*, and is the only other larval *Cyclothone* species found in abundance in the central gyre (Loeb 1979b). Fifty-nine of the sixty larvae caught were from the upper 50 m, and maximum abundance was at 0-25 m (Table 3). Median standard lengths increased with depth but, due to the small sample sizes, significance of differences in size-frequency distributions could not be tested. No metamorphic stages were taken either in the stratified tows or among the 365 *Cyclothone* sp. A larvae taken in 0-300 m IKPT samples during other gyre cruises. Most of early larval development may occur at 0-50 m, with a subsequent rapid descent to the juvenile-adult depth ranges (500-900 m; Kobayashi 1973).

VINCIGUERRIA SPP.—*Vinciguerria nimbaria* was the second most abundant species caught (9% of all larvae). On a year-round basis it is the most abundant larval fish species taken in the gyre (Loeb 1979b). The larvae occurred in samples from 0 to 350 m (Figure 3b), but were consistently present (29 out of 30 samples) only between 25 and 75 m. Ninety percent of the estimated water column abundance was between 25 and 75 m (74% at 25-50 m). Abundances in replicate tows within the 25-50 m depth interval were significantly greater ($P<0.01$) than in any other interval (Table 3).

Samples from 25 to 100 m contained a wide range of larval sizes. However, median standard length increased with depth (Table 3) and cumulative size-frequency curves from 25-50 m and 50-75 m (Figure 5) were significantly different from each other. The proportion of metamorphosing individuals increased below 50 m (Table 4). These included the prometamorphic (white photophore), midmetamorphic (rapid body shape change), and postmetamorphic (photophore completion and body pigmentation) stages described by Ahlstrom and Counts (1958). All *V. nimbaria* present in 0-25 m samples were early larvae, as were most in the 25-50 m samples (only 3% from 25-50 m were pro- or midmetamorphic). In contrast, 75% from 50-75 m were in metamorphic stages. Size distribution at 75-100 m was essentially bimodal: 40% of the larvae were very small (3.5-6.0 mm) and 50% were metamorphic (10.5-17.5 mm). No juveniles or adults were taken.

Vinciguerria poweriae was much less abundant, and had a deeper distribution than did its congener; it occurred from 50 to 350 m (Table 3), with maximum abundance at 75-100 m. There was a trend for increased size with depth (Table 3). Only four metamorphosing individuals were caught.

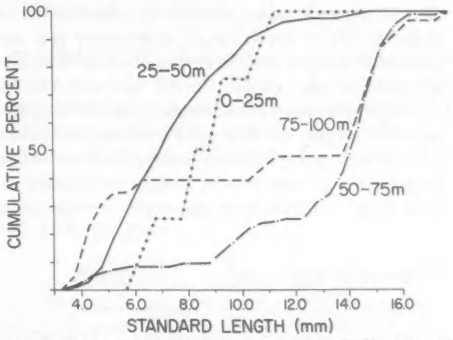

FIGURE 5.—Cumulative size-frequency curves for *Vinciguerria nimbaria* larvae by 25 m depth interval (10 samples per interval) within the upper 100 m of the North Pacific central gyre during summer.

TABLE 4.—Abundance of metamorphic stages of *Vinciguerria nimbaria* by depth during late summer in the North Pacific central gyre.

Depth interval (m)	Total individuals	Pro-	Mid-	Post-	Percent metamorphic
		metamorphic stages			
0-25	6				
25-50	376	5	6		2.9
50-75	99	25	15	34	74.7
75-100	25	2	4	7	52.0
100-350	1				

OTHER GONOSTOMATIDS.—The eight other gonostomatid species caught were rare; together <4% of the family total (Tables 2, 3). *Diplophos taenia* had the shallowest distribution of any gonostomatid species, occurring mostly at 0-25 m. *Gonostoma atlanticum, G. elongatum, Ichthyococcus ovatus*, and *Woodsia* sp. were present in the 75-350 m range, with maxima at 75-100 m. *Margrethia obtusirostra* and *Valenciennellus tripunctulatus* were caught only at 100-225 m and 100-350 m.

Family Sternoptychidae

The Sternoptychidae is the third most abundant family in the central gyre in terms of total larval abundance on a year-round basis (Loeb 1979b). Peak abundances occur during winter months, when this family makes up more than 6% of the total larvae. Minimal catches occur in late summer, so the 40 individuals taken during the present (late summer) cruise can provide only a very sketchy description of the vertical distributions of this otherwise abundant family.

The two genera (*Sternoptyx* and *Argyropelecus*) almost always occurred deeper than 100 m (Figure 2) and were abundant relative to other larvae in the 100-600 m depth range. *Sternoptyx* spp. appeared to have a shallower distribution than *Argyropelecus* spp. (Table 2). All but 2 of the 35 *Sternoptyx* larvae were taken between 100 and 350 m, with largest catches at 100-225 m (24 larvae distributed among all six samples). Four of the five *Argyropelecus* larvae were caught at 350-600 m. This is in contrast with the depth distributions found in the eastern Atlantic (Badcock and Merrett 1976) where *Argyropelecus* larvae were found from 100 to 500 m and *Sternoptyx* from 500 to 1,000 m.

A variety of developmental stages of both genera were found in the stratified samples. *Sternoptyx diaphana* from 100 to 225 m ranged from early larvae (3.8 mm) to larvae with abdominal and isthmal photophores (7.7 mm). The four *Argyropelecus* spp. from 350-600 m ranged from very small undeveloped larvae to one individual with an almost complete photophore complement.

Family Myctophidae

The myctophids (14 genera, 31 species) contributed over 42% of the total larvae. Over 98% of the estimated water column abundance was in the upper 100 m with maximum abundance at 25-50 m (Figure 6a). Diversity was highest (21 to 23 species) between 25 and 100 m (Table 2). The larval depth distributions of the two subfamilies differed (Figure 6b). Ninety-four percent of the Lampanyctinae estimated water column abundance was in the upper 75 m, with peak abundance at 25-50 m; only two (*Lobianchia gemellari* and *Notolychnus valdiviae*) of the 19 species were not taken in the 25-50 m interval (Table 3). This subfamily contributed 78% of the myctophid individuals and therefore greatly influenced the shape of the family distribution curve (Figure 6a). Myctophinae larvae were never caught in the upper 25 m, and contributed only 7% of the total myctophid larvae in the 25-50 m interval. The subfamily was most abundant from 50-225 m, contributing 49%, 58%, and 71% of the total myctophid larvae in the 50-75 m, 75-100 m, and 100-225 m intervals, respectively; peak abundance occurred at 50-75 m (Figure 6b). Only 4 of the 12 myctophine species taken were found at 25-50 m, while 7 were taken at 50-75 m and 11 at 75-100 m (Table 3). Significant differences were found between the cumulative frequency versus depth distributions of the two subfamilies (Kolmogorov-Smirnov test, $P<<0.01$).

Aspects of abundance, size distributions, and development of the more abundant species are considered below. For some species a variety of developmental stages was found. Because of the diverse patterns of photophore development exhibited by myctophid larvae (Moser and Ahlstrom 1970) only very general terminology is used to denote these stages. These include: early larvae (=

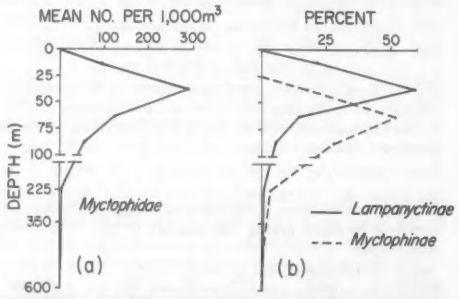

FIGURE 6.—Vertical distributions of larval myctophids in the North Pacific central gyre during summer. (a) Concentrations of myctophid larvae (31 species combined) by depth interval. (b) Percent of estimated water column abundances of Lampanyctinae and Myctophinae larvae in each depth interval.

no photophore development); early photophore development larvae (= photophores developing); late photophore development larvae (= lacking full photophore complement and still having larval morphology); transforming, or metamorphosing, individuals (= those completing photophore development and undergoing changes in pigmentation and morphology); and transformed, or early juvenile, stages (= adult morphology and photophore patterns, but still lightly pigmented). Additional information from other gyre cruises on developmental stages is included here.

Subfamily Lampanyctinae

BOLINICHTHYS SPP.—*Bolinichthys longipes* was the fifth-ranked species taken, occurring primarily in the upper 50 m, with peak abundance at 0-25 m; abundances in replicate tows within the 0-25 m interval were significantly greater (Mann-Whitney U test, $P<0.01$) than in other depth intervals (Table 3). Median standard lengths increased with depth (Table 3) and 0-25 m and 25-50 m cumulative size-frequency curves were significantly different from each other. The largest specimen (8.7 mm, from 50-75 m) was still in early photophore development. The largest *B. longipes* larva (10.8 mm) of the 670 taken from IKPT samples was also in early photophore development. No transforming individuals were taken, although juveniles ≥12.8 mm were caught.

Bolinichthys distofax had a narrower distribution than did *B. longipes*; all individuals came from 25-50 m (Table 3). Larval size ranges and developmental stages found in bongo and IKPT samples were comparable with those of *B. longipes*.

CERATOSCOPELUS WARMINGI.–*Ceratoscopelus warmingi* was the third-ranked species, >5% of total larvae, and is also third-ranked species on a year-round basis (Loeb 1979b). Although present at 0-225 m (Figure 7), 94% of the estimated water column abundance was at 25-75 m. Abundances in replicate samples within the 25-50 m interval were significantly greater ($P<0.01$) than in other intervals; the species made up 9% of the total larvae in this interval. Median standard lengths increased with depth and cumulative size-frequency curves for 0-25 m, 25-50 m, 50-75 m, and 75-225 m (Figure 8) were all significantly different from each other. The three largest larvae (8.6-12.8 mm), taken at 75-225 m, were still in early photophore development stages. No later photophore development stages or transforming specimens of *C. warmingi* were found among the 1,806 larvae (to 16.7 mm) examined from 0-300 m IKPT samples; a few early juveniles (≥18.0 mm) were taken.

DIAPHUS SPP.—Seven *Diaphus* species were taken on this cruise. They fell into the two morphological categories described by Moser and Ahlstrom (1974): the "slender" form (which as adults possess a suborbital photophore) and the

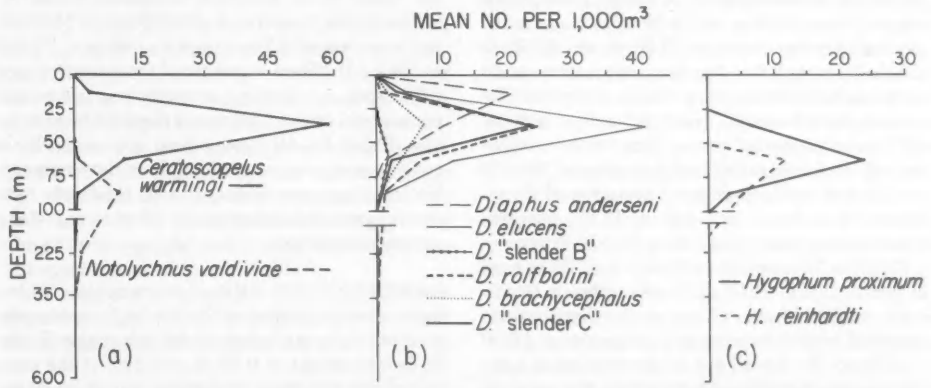

FIGURE 7.—Vertical distributions of various myctophid species in the North Pacific central gyre during summer. Concentrations of (a) *Ceratoscopelus warmingi* and *Notolychnus valdiviae*, (b) *Diaphus* spp., and (c) *Hygophum* spp. larvae by depth interval.

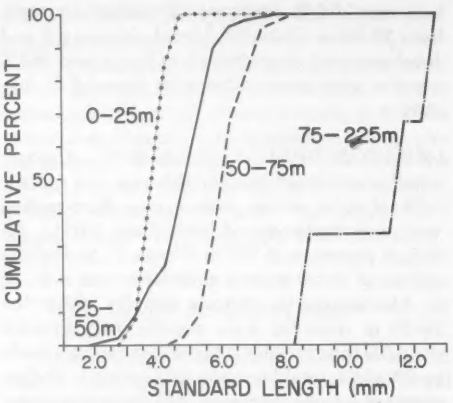

FIGURE 8.—Cumulative size-frequency curves for *Ceratoscopelus warmingi* larvae taken in 10 samples each from 0-25 m, 25-50 m, 50-75 m, and in combined samples from 75-100 m (10) and 100-225 m (6) of the North Pacific central gyre during summer.

"stubby" form (without this photophore). The presence of transforming specimens of most of these species in plankton samples facilitated their probable identifications. The "slender" species were *D. anderseni*, *D. brachycephalus*, and the *D. mollis* complex. The "stubby" species were *D. elucens*, *D. rolfbolini*, and the possible larvae of *D. schmidti*.

Diaphus anderseni had the shallowest distribution among *Diaphus* species, with 96% of the abundance from the upper 50 m and significant ($P<0.05$) peak abundance at 0-25 m (Figure 7b; Table 3). Median standard lengths increased slightly from 0-25 m to 25-50 m, with a much greater increase between 25-50 m and 50-75 m (Table 3); cumulative size-frequency curves were significantly different for all three intervals. The largest individuals (11.3 and 11.6 mm), caught at 50-75 m, were transforming. One recently transformed (10.5 mm) individual was taken at 100-350 m. The entire developmental sequence of *D. anderseni* was found in 0-300 m IKPT samples; transforming individuals were 11.3-11.8 mm.

Diaphus "slender C" (probably the "B" form of *D. mollis*; Clarke 1973), *D. brachycephalus*, *D. elucens*, and *D. rolfbolini* all had similar distributions centered around maximum abundances at 25-50 m (Figure 7b); for all but *D. brachycephalus* the abundances in replicate tows within this interval were significantly greater than in other depth intervals (Table 3). Within the 25-50 m interval, *D. elucens*, *D. rolfbolini*, and *D.* "slender C" ranked 4, 7, and 8, respectively, in total larval abundance; *D. elucens* was the fourth-ranked species taken overall during this cruise (Table 2). For each species, median standard lengths increased with depth (Table 3) and 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other.

No transforming individuals of these species were taken in tows considered here, although a transforming *D.* "slender C" (10.5 mm) was caught in a 0-100 m sample, and one recently transformed *D. elucens* (11.8 mm) was caught at 0-25 m. Oblique IKPT hauls (ranging in depth from 0-180 m to 0-360 m) on other central gyre cruises have caught late larval, transformational, and early juvenile stages of all four species. Transforming individuals of *D. brachycephalus* were 9.8-10.5 mm; *D. elucens*, 10.3-11.7 mm; *D.* "slender C," 11.2-12.7 mm; and *D. rolfbolini*, 11.7-12.5 mm.

The two other *Diaphus* species taken were both rare in stratified tows (Table 2). Most of *D.* "slender B" (probably the "A" form of *D. mollis*; Clarke 1973) occurred at 50-75 m, the deepest distribution of the genus (Figure 7b). Transforming specimens (10.0-11.3 mm) have been caught in 0-300 m IKPT hauls. *Diaphus* "stubby C" may be the larval form of *D. schmidti*; the larvae have been taken in the central gyre only in small numbers and sizes. Most were caught at 25-50 m during this cruise.

LAMPADENA SPP.—*Lampadena anomala* and *L. luminosa* were caught in low numbers within the upper 50 m. Eleven *L. luminosa* larvae occurred in four tows from both 0-25 m and 25-50 m; one large larva (12.7 mm) was also taken at 75-100 m (Table 3). There was a trend for increased size with depth. *Lampadena anomala* was taken (one per sample) in five 0-25 m and three 25-50 m samples (Table 3). All *Lampadena* spp. individuals were in early stages of photophore development. No late-stage specimens of these relatively rare central gyre species have been taken in any of the samples examined.

LAMPANYCTUS SPP.—*Lampanyctus steinbecki*, most abundant of the larval *Lampanyctus* species taken, ranked ninth for this cruise (Table 2). It was caught at 0-75 m, but 89% of the estimated water column abundance was at 25-50 m; abundances in replicate samples within this interval were significantly higher ($P<0.01$) than

in other intervals (Table 3). Only early-stage larvae (2.1-6.9 mm) were taken. Median standard length increased only slightly with depth (Table 3).

The three other *Lampanyctus* species caught in stratified tows were rare. These included: *L.* "big snout," probably of the *L. niger* complex; *L.* "lacks pectorals," a larval stage of an undescribed *Lampanyctus* species (E. H. Ahlstrom[3]); and *L. nobilis*. The larvae of *L.* "big snout" and *L. nobilis* were most abundant at 25-50 m, while *L.* "lacks pectorals" was taken mostly at 50-75 m (Table 3). All three species showed a trend for increased size with depth (Table 3); only early photophore development stages were taken. No late larval or transformational stages of any *Lampanyctus* species were found in 0-300 m IKPT samples (1,477 specimens examined).

LOBIANCHIA GEMELLARI—The larvae of *L. gemellari* occurred deeper than most lampanyctine species, only at depths >50 m (Table 3). Over 94% of the estimated water column abundance was between 50 and 100 m; larvae were similar in frequency of occurrence in samples and in abundance at 50-75 m and 75-100 m. Cumulative size-frequency curves for 50-75 m and 75-100 m were significantly different from each other and indicated more small and fewer large individuals in the deeper interval. The largest larvae taken in stratified tows (6.7 and 7.9 mm) were in early photophore development. Stages from early larvae through transformation (10.8-12.7 mm) were caught in 0-180 m IKPT hauls.

NOTOLYCHNUS VALDIVIAE.—Both the adult and larval *N. valdiviae* differ from other lampanyctine species in several respects, and Moser and Ahlstrom (1974) suggested placement of the species in a separate subfamily. The larvae are also unusual in their depth distributions as compared with other lampanyctine species (Figure 7a). *Notolychnus valdiviae* was absent at 0-50 m and rare at 50-75 m; maximum abundance (40 of the 44 larvae caught) occurred at 75-100 m where the species ranked fourth (Table 2).

All stages of development of *N. valdiviae* were found between 50 and 100 m. The largest pretransformation specimen (8.0 mm) was from 75-100 m. A 10.5 mm transforming specimen plus nine other individuals ranging from recently transformed to adult (10.8-21.8 mm) were caught at 50-75 m. Three other metamorphosed individuals were found in other intervals: a recently transformed individual (11.3 mm) at 25-50 m; and two juveniles (15.7 and 17.3 mm) at 75-100 m.

TRIPHOTURUS NIGRESCENS.—*Triphoturus nigrescens* was the fourth-ranked myctophid (eighth ranked species overall) taken. The larvae were distributed from 0 to 100 m, with 88% of the estimated water column abundance at 25-50 m; abundances in replicate samples within this interval were significantly greater ($P<0.01$) than in other intervals (Table 3). Median standard lengths increased below 50 m (Table 3) and 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other. The 11.8 mm larva, from 75-100 m (Table 3), was one of the largest *T. nigrescens* larvae taken in any central gyre plankton sample; it still lacked photophore development. Nine metamorphosed individuals were also caught in stratified tows: six (14.7-17.0 mm) at 25-50 m; one (17.9 mm) at 50-75 m; and two (17.0 and 21.3 mm) at 75-100 m. No late-stage larvae have been found among the 612 specimens collected from central gyre IKPT samples.

Subfamily Myctophinae

BENTHOSEMA SUBORBITALE.—*Benthosema suborbitale* occurred at 75-350 m, and was an important component of the deeper ichthyoplankton, ranking third in 75-100 m samples and second in 100-225 m and 100-350 m samples (Table 2). Largest numbers occurred at 75-100 m, but 46 of the 48 larvae from this interval came from only 2 of 10 samples; frequency of positive samples was highest at 100-225 m (five of six samples). Size ranges, median lengths, and cumulative size-frequency curves were similar for all depth intervals. The largest larva (8.0 mm) was in early photophore development. Seven recently transformed juveniles were caught: five (11.1-12.1 mm) at 25-50 m and two (10.8 and 12.7 mm) at 50-75 m. Developmental stages to early transformation (10.8-11.3 mm) were found in 0-300 m IKPT samples.

CENTROBRANCHUS SPP.—Three species of *Centrobranchus* were caught at 75-100 m (Table

[3]E. H. Ahlstrom, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, pers. commun. 1977.

3). *Centrobranchus andrae* and *C. brevirostris* were represented by single specimens. The five *C. choerocephalus* individuals (3.4-7.1 mm) occurred in three samples. All specimens were early photophore stage larvae.

DIOGENICHTHYS ATLANTICUS.—The 12 *D. atlanticus* larvae (all early photophore stage larvae) were caught between 75 and 350 m; 8 came from 75-100 m (Table 2). During other central gyre cruises, *D. atlanticus* was abundant in IKPT samples, and developmental stages from early larvae to transformation (11.3-12.8 mm) were found.

HYGOPHUM SPP.—*Hygophum proximum* was the most numerous larval myctophine (Table 2). It occurred from 25 to 100 m, with maximum abundance and significantly larger catches in replicate tows ($P<0.01$) at 50-75 m (Table 3). Median standard length increased with depth (Table 3) and 25-50 m and 50-100 m size-frequency curves were significantly different from each other. The largest larva (10.0 mm, from 75-100 m) was in early photophore development. No late-stage *H. proximum* larvae have been found among the 490 examined from 0-300 m IKPT samples.

Hygophum reinhardti larvae were more deeply distributed than those of *H. proximum*, occurring from 50 to 225 m. As with its congener, maximum estimated water column abundance and significantly larger catches ($P\leq0.05$) were at 50-75 m, but the larvae were also frequently taken (7 of 10 samples) at 75-100 m (Figure 7c). There were no apparent trends in size with depth (Table 3). No late photophore development larvae were caught, but two recently transformed individuals (12.3-13.3 mm) were found in 0-300 m IKPT samples from other cruises.

MYCTOPHUM SPP.—Four *Myctophum* species were caught (Table 2). The 58 *M. lychnobium* larvae occurred between 25 and 100 m, with maximum abundance at 25-50 m; *M. brachygnathum* had a similar distribution. All five *M. selenops* were caught at 50-75 m, and six of the seven *M. nitidulum* at 75-100 m. All of the larvae were small (<8.0 mm) and in early photophore development; only those of *M. brachygnathum* appeared to have increased size with depth (Table 3). A total of 393 *Myctophum* larvae, of all four species, have been examined from central gyre IKPT samples; none exceeded 10.0 mm or were in advanced stages of photophore development.

SYMBOLOPHORUS EVERMANNI.—*Symbolophorus evermanni* occurred from 25 to 225 m; over 90% of the estimated water column abundance was between 50 and 100 m; abundances in replicate samples within the 50-75 m interval were significantly greater ($P<0.05$) than in other intervals (Table 3). Although the largest larva (10.5 mm) was from 75-100 m, the median standard length was smaller there than at shallower depths (Table 3). The 25-50 m and 50-75 m cumulative size-frequency curves were significantly different from each other, indicating decreased size with increased depth. Only early photophore development stages were caught by stratified tows. This was also the case for all 0-300 m IKPT samples examined, where the largest prejuvenile (15.5 mm) of 369 individuals was in the earliest stages of photophore development.

Other Larvae

Other families contributed only 9% of the identified larvae and included a wide assortment of mesopelagic fishes; only 3 of the 33 families identified were epipelagic. These "other larvae" were found in samples taken from 0 to 350 m (Figure 2). Total abundance was low in the upper 75 m, but increased greatly below 75 m (due primarily to peak abundances of two families), and made up 25% and 19% of the ichthyoplankton in 75-100 m and 100-350 m samples, respectively. Maximum diversity occurred at 25-50 m.

None of these "other" species was abundant. Of the 49 kinds of larvae represented only 3 were caught in even moderate numbers: *Bregmaceros* spp. (Bregmacerotidae), *Odontostomops normalops* (Evermannellidae), and *Howella* sp. (Aponogonidae). Only *Bregmaceros* spp. is abundant in the central gyre ichthyoplankton on a year-round basis (Loeb 1979b). Together these three kinds made up 39% of the other larvae; the remaining 61% was contributed by 1 order and 30 families (42 species). Catch information on the other larvae is presented in Table 2; more detailed distributional data is provided in Loeb (1979a).

DISCUSSION AND CONCLUSIONS

The overall vertical distribution pattern of central gyre ichthyoplankton conforms to that described by Ahlstrom (1959) for the California Current. Most species and individuals were in the upper 100 m, with maximum abundance and di-

versity at 25-50 m, possibly related to the bottom of the mixed layer. A distinct change in species composition and relative abundances occurred below 75 m. This involved a shift from dominance by *Cyclothone alba, Vinciguerria nimbaria*, and lampanyctine myctophids to other gonostomatid species, myctophine myctophids, and other families. Ahlstrom (1959) previously had found groups of species (in the California Current) to be either predominantly within the mixed layer and upper thermocline or mostly within or below the thermocline.

None of the abundant larvae were taken only in one 25 m interval, and most were found over at least a 75 m depth range. However, almost all species taken in the upper 100 m had distinct maxima of catch frequency and abundance within one of the 25 m depth intervals sampled; for many species, despite high catch variability due to patchiness, the abundances in replicate tows within this interval were significantly higher than in any other interval. Almost twice as many larvae and half again as many kinds were found in 100-225 m samples as in 100-350 m samples, indicating that most deeper species may be distributed above 225 m.

Significant changes were found in cumulative size-frequency distributions with depth for many of the abundant species. There was a general trend for those species with peak abundance in the upper 50 m to have significant increases in larval size with depth. Species with maximum abundance below 50 m tended to exhibit no size-depth changes, or had significant decreases in size with depth. With these deeper larvae, the apparent lack of size change with depth may be the product of small sample sizes outside the depth of maximum abundance and the broader depth ranges sampled below 100 m.

The gonostomatids exhibited two different distributional patterns. *Cyclothone* spp., *V. nimbaria*, and *Diplophos taenia* occupied the topmost 50 m. The other seven species were distributed below 75 m, with maximum abundances in the 75-225 m range. The nighttime depth distribution patterns of juveniles and adults (from Clarke 1974) of the migratory gonostomatid species relative to each other are, with the exception of *Gonostoma elongatum*, generally the same as for the larvae (Figure 9). Both larval and adult *Diplophos taenia* had the shallowest distribution and *Valenciennellus tripunctulatus* the deepest distribution within the family. Also, except for *G. elongatum*,

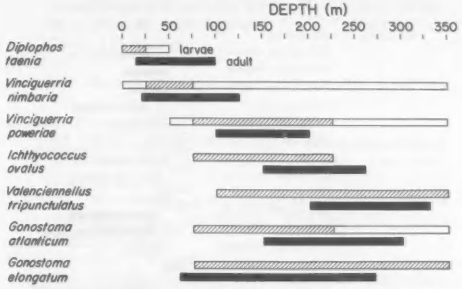

FIGURE 9.—Larval (upper bar) and adult (lower bar) nighttime depth distributions for migratory gonostomatid species taken in late summer near lat. 28° N, long. 155° W (North Pacific central gyre). Hatched larval depth range indicates intervals where >90% of the estimated water column abundance occurred. Adult depth distributions from Clarke (1974).

the upper depth distributions of the adults (usually small adults; Clarke 1974) tend to overlap the lower ranges of peak larval abundance. Although Clarke's (1974) adult information is from a different oceanic regime (offshore Hawaiian waters), his general patterns of depth distribution may still be valid for the central gyre adults.

The night depth patterns of larval and adult myctophid species are more complex than those of the gonostomatids. The larvae of subfamily Lampanyctinae generally occupy shallower depths than do those of subfamily Myctophinae (Figure 6b). The opposite is generally true of the night distributions of the adults from the two subfamilies. Clarke (1973) presented adult depth distributions for 46 myctophid species taken near Hawaii. Of the 15 myctophine species he listed, 8 had upper night distribution limits at 0-25 m (5 of these were taken in substantial numbers by dip nets); 2 others occurred at 25-50 m. In contrast, only 10 of the 31 lampanyctine species listed by Clarke (1973) were caught in the upper 50 m. Ahlstrom and Stevens (1976) also found that neuston (surface) samples taken in the California Current caught only myctophine juveniles and adults and lampanyctine larvae.

Different night adult and larval depth patterns are apparent for the two subfamilies (Figure 10). Lampanyctine adults, generally overlap, or are distributed below, their depths of maximum larval abundance. The shallowest lampanyctine individuals (which share the larval depth range) are usually small adults or juveniles (Clarke 1973). This contrasts strongly with myctophine adults

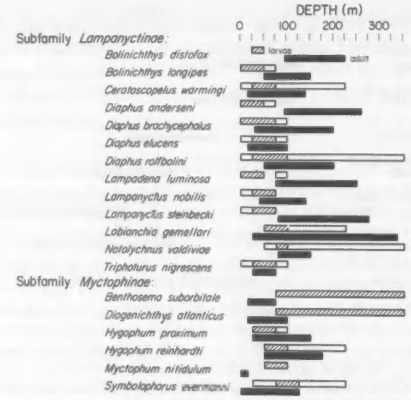

FIGURE 10.—Larval (upper bar) and juvenile and adult (lower bar) nighttime depth distributions for the more abundant lampanyctine and myctophine (Myctophidae) species taken in late summer near lat. 28° N, long. 155° W (North Pacific central gyre). Hatched larval depth range indicates depth intervals where ≥90% of the estimated water column abundance occurred. Adult depth distributions from Clarke (1973).

(except for *Hygophum* spp.), wherein all sizes tend to be distributed above the depths of maximum larval abundance. In most cases the largest adults of both subfamilies are vertically separated from the larvae, and, where overlap occurs, the smallest juveniles are in similar depth ranges with the largest larvae.

A variety of patterns of early developmental stages were found. Among the gonostomatids, metamorphic stages of *Cyclothone alba* and *Vinciguerria* spp. were found in stratified samples. Apparently *C. alba* leaves the larval depth range once it has reached the prometamorphic stage of development. *Vinciguerria* spp. go through all early metamorphic stages while in the larval depth range and presumably descend to greater depths once the postmetamorphic stage is completed. For both *C. alba* and *V. nimbaria* the advanced stages of larval development were found in the lower portion of the larval depth range. Gradual downward migration with development, as seen in *V. nimbaria*, may also occur in *Valenciennellus tripunctulatus* and *Gonostoma* spp. (Badcock and Merrett 1976).

The myctophid species exhibited different levels of photophore development before descending to juvenile depths. Developmental series from early larvae to transforming individuals were found from ≤350 m for 11 of the 31 myctophid species taken in Climax I. These include: six of the seven *Diaphus* species (all but *D. schmidti*), *Lobianchia gemellari, Notolychnus valdiviae, Benthosema suborbitale, Diogenichthys atlanticus,* and *Hygophum reinhardti*. At least some individuals of *Diaphus* spp., *L. gemellari, N. valdiviae,* and *D. atlanticus* complete transformation before descent to juvenile depths or else begin extensive migrations before transformation. The presence of lightly pigmented juveniles of *D. anderseni, D. elucens, N. valdiviae, B. suborbitale,* and *H. reinhardti* in the upper 100 m at night indicated that, if these are not predescent individuals, some members of these species may undergo early juvenile migration.

No late photophore stage larvae were found for *Bolinichthys* spp., *Ceratoscopelus warmingi, Lampadena* spp., *Lampanyctus* spp., *Triphoturus nigrescens, H. proximum, Myctophum* spp., or *Symbolophorus evermanni* in either the Climax I samples or 0-300 m IKPT samples taken on other gyre cruises. These larvae appear to leave the upper 300 m of the water column at varying levels of early photophore development prior to transformation. The late stages of photophore development probably occur at the juvenile day depth range for each species. The developmental state at descent appears to be a generic characteristic within both subfamilies. Except for *Hygophum* spp., congeners achieved similar levels of photophore development while in the upper 300 m.

Due to small numbers of other larvae captured, little can be ascertained about their distributional patterns. Most species occurred in the upper 100 m, with greatest numbers of species at 25-50 m. Basic trends in depth distribution appeared to exist on a familial or ordinal level: Notosudidae were most abundant at 0-25 m; five families of ceratioid fishes occurred in the upper 50 m; four families of stomiatoid fishes and the Evermannellidae occurred most frequently at 25-75 m; Bregmacerotidae and Melamphaeidae were most abundant at 75-100 m; and Scopelarchidae, Bathylagidae, and Sternoptychidae occurred below 100 m. The paralepidids (much like the myctophids) exhibited a variety of depth distributions through the upper 225 m.

The depth distributions described are for the late summer central gyre ichthyoplankton assemblage. Surface temperature is 6°-7° C lower in winter and the mixed layer depth increases from ca. 40 m in late summer to 110-140 m in winter (McGowan and Williams 1973). There are also

definite seasonal changes in larval fish species composition and abundance relations. As larval depth distributions are apparently affected by temperature distribution and mixed layer depth (Ahlstrom 1959) spatial patterns in winter gyre waters may be different from those portrayed here.

ACKNOWLEDGMENTS

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RESISTANCE OF DIFFERENT STOCKS AND TRANSFERRIN GENOTYPES OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, AND STEELHEAD TROUT, *SALMO GAIRDNERI*, TO BACTERIAL KIDNEY DISEASE AND VIBRIOSIS[1]

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ABSTRACT

Juvenile coho salmon and steelhead trout of different stocks and three transferrin genotypes (AA, AC, and CC), all reared in identical or similar environments, were experimentally infected with *Corynebacterium* sp., the causative agent of bacterial kidney disease, or with *Vibrio anguillarum*, the causative agent of vibriosis. Mortality due to the pathogens was compared among stocks within a species and among transferrin genotypes within a stock to determine whether there was a genetic basis for resistance to disease. Differences in resistance to bacterial kidney disease among coho salmon stocks had a genetic basis. Stock susceptibility to vibriosis was strongly influenced by environmental factors. Coho salmon or steelhead trout of one stock may be resistant to one disease but susceptible to another. The importance of transferrin genotype of coho salmon in resistance to bacterial kidney disease was stock specific; in stocks that showed differential resistance of genotypes, the AA was the most susceptible. No differences in resistance to vibriosis were observed among transferrin genotypes.

Bacterial kidney disease (BKD) caused by *Corynebacterium* sp. is a major cause of serious losses among salmon reared in freshwater hatcheries of the Pacific Northwest (Leitritz and Lewis 1976), and epizootics caused by *Vibrio anguillarum* in the marine environment are particularly devastating to salmonids maintained in saltwater impoundments (Fryer et al. 1972). Externally applied antibiotics are relatively ineffective in the treatment of these diseases. Immunization with bacterins for the control of vibriosis has been shown to be feasible (Fryer et al. 1976), but attempts to produce a bacterin for BKD have been unsuccessful (Evelyn 1977). The use of disease resistant populations of fish may conceivably reduce the incidence and severity of these diseases. Fish that inherit natural resistance to a disease normally maintain that resistance throughout their lives (Snieszko et al. 1959). In addition, information on the resistance of donor stocks, for use in transplants to infected waters, would be valuable.

The existence of disease resistant strains within a species has been demonstrated. Stock or strain refers to a population of fish of one species which shares both a common environment (a particular stream) and common gene pool (discrete breeding group) and, as such, can be considered as a self-perpetuating system (Larkin 1972). Differences in susceptibility to ulcer disease and furunculosis have been observed among different strains of brook trout, *Salvelinus fontinalis* (Wales and Berrian 1937; Wolf 1954; Snieszko 1957; Snieszko et al. 1959), and Gjedrem and Aulstad (1974) noted significant differences in resistance to vibriosis, which they showed to be slightly heritable, between different strains of Atlantic salmon, *Salmo salar*, parr in Norway. Unfortunately, in most previous studies of disease resistance, fish of the different stocks were not reared in a common environment. Since phenotypic expression is a combination of genotype, environment, and interactions between these two variables, different stocks must be reared under identical conditions if one is to be certain that differences in resistance to disease are genetic in origin and not due, for example, to previous exposure of a particular stock to the disease in question or some other factor such as nutritional history. One objective of the present study was to determine whether there are differences in resistance to BKD and vibriosis

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among stocks of coho salmon, *Oncorhynchus kisutch*, and steelhead trout, *Salmo gairdneri*, and whether these differences have a genetic basis.

Suzumoto et al. (1977) reported differences in resistance to BKD among three genotypes of transferrin (an iron-binding plasma protein) in coho salmon. In mammals, iron is known to increase the growth and virulence of some pathogens. Transferrin may reduce infection by binding the metal, thereby reducing its availability to invading bacteria, a process known as nutritional immunity (Weinberg 1974). No iron requirement has been demonstrated for BKD bacteria, although it is likely that one exists, judging by the fastidiousness of the organisms. Hershberger (1970) observed differences in iron binding capacity among transferrin genotypes in brook trout and suggested that individuals more efficient in the uptake and release of iron might fare better under "adverse conditions" such as disease. A second objective of this study was to compare resistance to BKD and vibriosis among transferrin genotypes, to evaluate earlier results with BKD, and to determine whether transferrin increases the tolerance of bacterial diseases of salmonids in general. We also sought to determine whether differences in resistance of transferrin genotypes exist among different stocks of coho salmon and steelhead trout.

MATERIALS AND METHODS

Juvenile coho salmon were obtained as eyed eggs from the Fall Creek (Alsea) and Big Creek salmon hatcheries, Oreg. The Big Creek hatchery was also the source of two crosses, Big Creek × Sol Duc (B × S) and Big Creek × Umpqua (B × U). All stocks were reared at Corvallis, Oreg.—the Big Creek stock at Oregon State University's Smith Farm; the Alsea stock at the Oregon Department of Fish and Wildlife's Research Section; and the two crosses at Oregon State University's Fish Disease Laboratory. These rearing facilities presented similar, though not identical, environments for the fish. Because we lacked sufficient fish of the two crosses to include them in all studies, we used them only in the BKD study.

Steelhead trout were obtained as green eggs from the following Oregon State hatcheries: Alsea (winter run), Roaring River (Siletz summer run), Cole Rivers (Rogue summer run), and Marion Forks (North Santiam winter run). All four stocks were reared under identical conditions at Smith Farm.

For determination of the transferrin genotypes of the experimental fish, we withdrew about 0.1 ml of blood from the caudal vein of anesthetized fish with a 1 ml tuberculin syringe and ejected it into heparinized hematocrit tubes, which were then centrifuged. The plasma from the salmon was frozen until the time of analysis. Blood samples from steelhead trout were placed on ice and processed within 4 h after collection because we found that frozen storage reduces the stability of transferrin in this species. Fish were individually identified by dangler tags applied immediately behind the dorsal fin. We used starch-gel electrophoresis, adapting the discontinuous buffer system described by Ridgeway et al. (1970), to determine transferrin genotypes. Only the AA, AC, and CC genotypes were considered, and in some stocks only two of these were used. The transferrins of Siletz and North Santiam steelhead trout stocks were not included in this study because resolution on the electrophoretic gels was poor. After the fish were bled, they were given a recovery period of at least 2 wk before they were transferred to experimental tanks.

Bacterial Kidney Disease

All experimental fish were held indoors in 70 l fiber glass tanks supplied with flowing, aerated, chilled (12°±2° C), dechlorinated water. The fish were allowed to acclimate in these tanks for 2 wk. Fish were fed once daily with Oregon Moist Pellet. Each stock of coho salmon and steelhead trout consisted of 125 fish divided into two test replicates of 50 each plus 25 control fish. Included in the steelhead trout experiment was one group of 34 fish of hatchery-reared (Cole Rivers) Rogue River stock, without a replicate. The respective transferrin genotypes were distributed randomly among all tanks.

The BKD (*Corynebacterium* sp.) strain (RB-1-73) used was isolated on cysteine serum agar from a spring chinook salmon, *O. tshawytscha*, at the Round Butte Oregon State Hatchery by J. E. Sanders, fish pathologist, Oregon Department of Fish and Wildlife. A stock culture was maintained on Mueller-Hinton agar (Difco Laboratories,[4] Detroit, Mich.) enriched

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

with cysteine (0.1%) and calf serum (20%). Before each experiment, cells were passed once in the species being tested to produce a fresh isolate, and this isolate was further cultured until sufficient cells were available for an inoculum.

All test fish received an intraperitoneal injection of 0.1 ml of a suspension of kidney disease bacteria in phosphate-buffered saline (PBS), and all control fish received a 0.1 ml intraperitoneal injection of only PBS. The approximate inocula were 9×10^7 cells for the coho salmon (mean weight, 23 g), and 3×10^8 cells for the steelhead trout (mean weight, 36 g). The coho salmon were injected on 17 March 1977 and the steelhead trout on 12 September 1977. We examined all fish that died and identified BKD as the causative agent on the basis of presumptive diagnosis, using gram stains of kidney smears. In addition, kidney smears from 10% of the fish that died were cultured on Mueller-Hinton media. Experiments were terminated at the end of 4 mo or earlier, depending on the progress of infection.

One week after the coho salmon had been injected, an accidental exposure of the fish, including the controls, to chlorine resulted in mortalities as high as 50% in some stocks. The study was nevertheless continued, but a second, abbreviated test was begun on 24 August 1977. Only Alsea and Big Creek stocks (mean weight, 33.2 g) were used; the Big Creek fish were obtained directly from the hatchery. The inoculum for this second experiment was increased to 3×10^8 cells.

Vibriosis

The *V. anguillarum* strain (LS-174) used in these experiments was isolated on brain heart infusion agar from a coho salmon at Lint Slough, Waldport, Oreg., by J. S. Rohovec. The inocula were either prepared from lyophilized cells or recent passage isolates. Experimental fish were exposed to the pathogen in 93 l stainless steel tanks at Oregon State University's Fish Disease Laboratory.

Two experiments were undertaken with the coho salmon. In the first (8 October 1976), 225 fish (mean weights for Big Creek and Alsea stocks were 10.4 g and 14.5 g, respectively) from each stock were divided equally among two test replicates and an untreated control. The three tanks contained fish from each stock to insure identical treatment. The fish in this experiment, having not been bled and tagged for transferrin genotype identification, were freeze branded to differentiate the stocks in each tank. In the second experiment (10 June 1977) the number of fish per tank was reduced to about 25 (mean weight, 36.6 g) because larger numbers were not available, but transferrin genotypes had been determined.

In the steelhead trout phase of the study (21 October 1977), 75 fish from each stock (mean weight, 36 g) were divided equally among three test replicates and 15 from each stock were placed in a fourth tank for controls. A hatchery-reared Rogue stock was also used in this steelhead trout experiment. In a second experiment (27 December 1977) in which we used steelhead trout from the Cole Rivers (Rogue), Alsea, and Marion Forks (North Santiam) hatcheries, 50 fish (mean weight, 42.2 g) were divided equally between two replicates. Transferrin genotypes were distributed randomly among the tanks.

The initial temperature in all experimental tanks was 12.2° C, to which all fish had been acclimated. The temperature was then raised to 17.7° C over a period of 1.5 h, and at this temperature water flow was discontinued in all tanks for 15 min. The bacteria suspended in brain heart infusion broth (Difco Laboratories) were then introduced into the test tanks (other than those of the controls). The inocula were 5×10^6 cells/ml for the first coho salmon exposure and 8.6×10^6 cells/ml for the second; the steelhead trout received concentrations of 8.8×10^6 cells/ml in the first experiment and 7.2×10^6 cells/ml in the second. All fish that died were necropsied and kidney smears were cultured on brain heart infusion agar. Positive diagnosis of *V. anguillarum* was confirmed by slide agglutination with specific antiserum. The experiments were terminated at the end of 1 wk.

Statistical comparison of three or more stocks involved a one-way analysis of variance based on arcsin transformations of percentages and least significant difference, and comparisons of transferrin genotypes of two stocks were based on χ^2 test employing a $2 \times k$ contingency table (Snedecor and Cochran 1967).

RESULTS AND DISCUSSION

Bacterial Kidney Disease

In the first experiment in which coho salmon were infected with BKD, the Alsea stock and B × U cross were about twice as resistant to the disease

as were fish of the Big Creek stock and B × S cross (see totals, Figure 1A). The difference in mortality between the B × U and each of the two more susceptible groups (Big Creek and B × S), was significant ($P<0.05$), but the Alsea mortality was significantly lower than that of only the B × S, cross ($P<0.06$). A comparison of mean times to death (days) revealed a similar pattern: B × S, 79.5; B × U, 99.9; Big Creek, 88.4; and Alsea, 95.4. The mean times to death for the B × U and Alsea coho salmon were significantly greater than the B × S ($P<0.05$). The differential resistance of coho salmon stocks to BKD probably has a genetic basis because the stocks were reared in similar environments.

Among transferrin genotypes, only the B × S cross and Alsea stock showed any important differences in resistance to BKD (Figure 1A). In both groups the AA genotype was the most susceptible, and the AC and CC both showed lower, similar mortalities. The difference in resistance was significant ($P<0.07$) between the AA and AC genotypes within the B × S cross. The Alsea transferrin results, though not significant due to small sample size, are substantiated by a previous study in which Suzumoto et al. (1977)

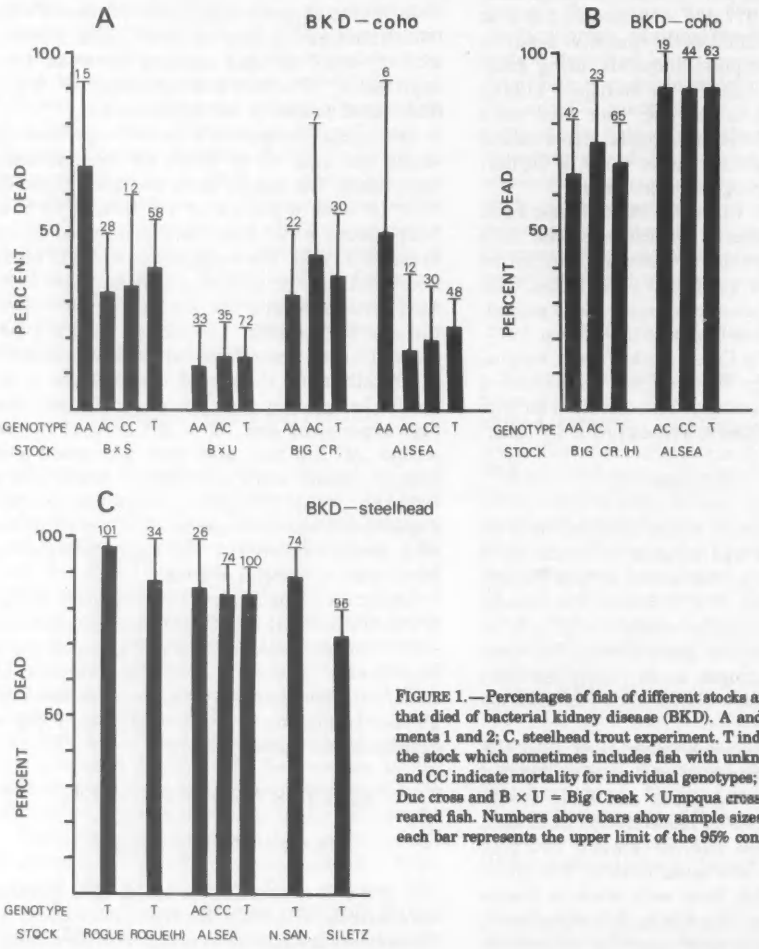

FIGURE 1.—Percentages of fish of different stocks and transferrin genotypes that died of bacterial kidney disease (BKD). A and B, coho salmon experiments 1 and 2; C, steelhead trout experiment. T indicates total mortality for the stock which sometimes includes fish with unknown genotypes; AA, AC, and CC indicate mortality for individual genotypes; B × S = Big Creek × Sol Duc cross and B × U = Big Creek × Umpqua cross; (H) indicates hatchery-reared fish. Numbers above bars show sample sizes; the vertical line above each bar represents the upper limit of the 95% confidence interval.

used Alsea coho salmon in which the AA genotype was also the most susceptible to BKD. Because of similar transferrin results in the B × S cross and Alsea stock, the data were combined. For the combined data, the AC (28% mortality) and CC (24% mortality) genotypes were significantly ($P<0.01$) more resistant to BKD than was the AA genotype (62% mortality). Within both the stocks and transferrin genotypes, differences between replicates were not significant.

The second BKD experiment with coho salmon gave results similar to those of the first on the basis of transferrin genotypes (Figure 1B). Unfortunately, the AA genotype was not included in the Alsea comparison because we lacked sufficient fish. No stock comparison was made because the Big Creek stock came directly from the hatchery, at a time when 91.5% of the mortalities in production fish at Big Creek were due to BKD (J. Conrad[5]). The probability that the Big Creek coho salmon used in the experiment had previously been exposed to BKD was therefore very high.

In the third BKD study, which involved the four steelhead stocks and a second Rogue stock reared at the hatchery (Figure 1C), mortalities in all the test groups began to increase at a high rate 3 wk after the study began because of a secondary infection with *Aeromonas hydrophila*. This trend continued for another 4 wk, at which time mortalities leveled off, and the study was terminated. A comparison of the resistance of the different stocks is not fully valid because the fish in the different test tanks were obviously not challenged equally with a secondary infection of *A. hydrophila*. However, there were no significant differences ($P>0.10$) between replicates, and the mortality of the Siletz steelhead trout (72%) was significantly lower ($P<0.05$) than that of all other stocks except the Alsea. Because mortality in the Rogue stock was extremely high (96%), a transferrin genotype comparison was not considered. The AC and CC genotypes within the Alsea stock were equally susceptible to the double infection of BKD and *A. hydrophila*. Although percentage mortality is a better measure of an organism's ability to tolerate disease, mean time to death is also an indication of resistance to diseases, especially chronic ones such as BKD. There were no differences in mean time to death (days) among either the Rogue or Alsea steelhead transferrin genotypes (numbers of fish in parentheses): Rogue—AA, 28.5 (30); AC, 30.0 (41); and CC, 29.7 (19); Alsea—AC, 30.4 (21); and CC, 30.0 (62). The importance of transferrin was probably reduced by the double infection.

[5]J. Conrad, Oregon Department of Fish and Wildlife, Clatskanie, OR 97015, pers. commun. February 1978.

Vibriosis

In the first experiment in which coho salmon were exposed to *V. anguillarum* (Figure 2A), the Big Creek stock (38% mortality) was significantly more resistant ($P<0.005$) than the Alsea stock (62% mortality) (transferrin was not considered in this comparison). There was a significant difference ($P<0.005$) in mean weight (t'-test, Snedecor and Cochran 1967:114) between the Alsea and Big Creek fish. However, there were no significant differences ($P>0.10$) in resistance to vibriosis among four weight classes (5.1-10.0, 10.1-15.0, 15.1-20.0, and 20.1-25.0 g) within either stock. The difference in resistance between the two stocks appears to be genetic. In a second test, the resistance trend between the Alsea and Big Creek stocks was reversed (Figure 2B), though at a lower level of significance ($P<0.07$) than the previous experiment. However, the Alsea coho salmon used in this second test came directly from the hatchery. Though it is unlikely that any of these fish would have been previously exposed to *V. anguillarum* in freshwater, a difference in susceptibility to vibriosis still existed. These conflicting results thus demonstrate that the environment has a strong effect in determining resistance to vibriosis. In both the Alsea and Big Creek stocks, no differential resistance was shown by the transferrin genotypes, although the AA genotype was not included in the Alsea transferrins (Figure 2B).

In the first of the two vibriosis experiments with steelhead trout (Figure 2C), the North Santiam steelhead trout were the least susceptible to vibriosis of all the stocks ($P<0.05$). The Alsea steelhead trout, though exhibiting a higher mortality (87%) than the North Santiam fish, were still significantly more resistant than the remaining two stocks ($P<0.05$). Because mortality was high in the Smith Farm- and hatchery-reared Rogue stocks (96%), transferrin genotype differences and the effects of rearing environment on resistance were not considered. However, no differences in resistance were observed among genotypes within the Alsea stock. These results using steelhead trout are similar to those observed in the coho salmon exposed to vibriosis.

The second vibriosis experiment (Figure 2D),

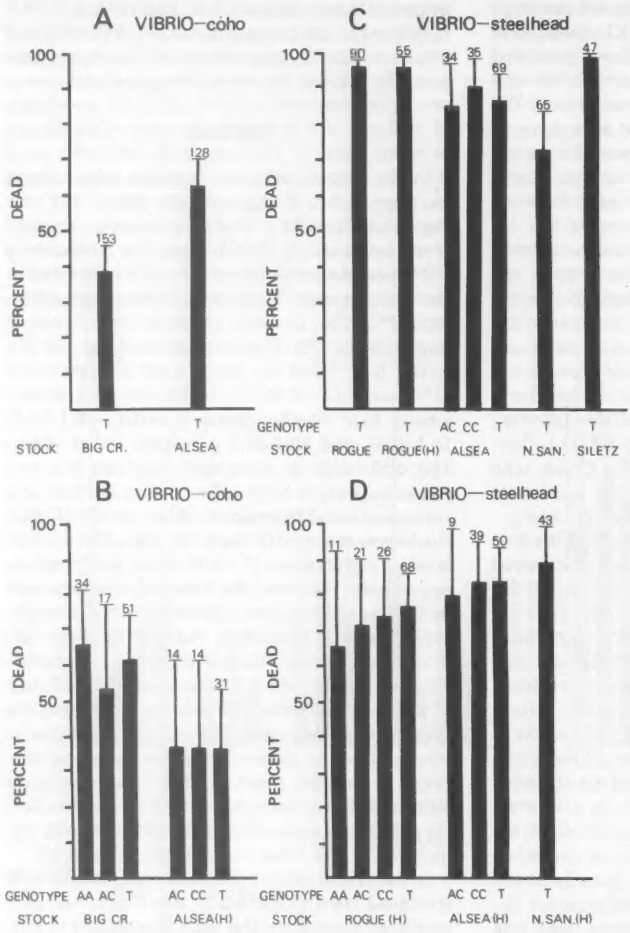

FIGURE 2.—Percentages of fish of different stocks and transferrin genotypes that died of vibriosis. A and B, coho salmon experiments 1 and 2; C and D, steelhead trout experiments 1 and 2. For interpretation of other features see Figure 1.

involving hatchery-reared steelhead trout from the Rogue, Alsea, and North Santiam, revealed the same results as did the first, with respect to transferrin genotypes. No differential resistance was shown among genotypes, including the AA's, within either the Alsea or Rogue stocks. Although resistance to vibriosis among the three stocks was similar, the North Santiam stock showed the highest mortalities this time—which again emphasizes the importance of environmental factors in the determination of resistance and the need for eliminating environmental differences in making genetic comparisons. There was a significant difference in vertebral number between North Santiam steelhead trout reared at the hatchery and at Smith Farm, indicating an environmental difference (our unpubl. data). The Rogue replicates in this experiment were significantly different ($P<0.025$) with respect to stock mortality; consequently a genetic comparison was invalid. Except for the hatchery-reared Rogue replicates in the last vibriosis experiment using steelhead trout, there were no significant differences between replicates for stocks or genotypes in all four vibriosis tests; consequently we combined replicates in the data analysis.

Perhaps stock resistance to acute diseases such as vibriosis depends more on which stock has an environmental advantage at the time of infection, rather than on genetic make-up. Also, when mortalities in experiments are high, resistance comparisons are difficult to make because any immunity that was present may have been overwhelmed. Genetic factors are probably more important in chronic diseases such as BKD. For example, Zinn et al. (1977) observed apparent genetic resistance to infection by *Ceratomyxa shasta,* normally not an acute condition, among hatchery strains of chinook salmon.

It is also evident that a stock may be resistant to one disease and not to another. Although the Siletz steelhead trout were most resistant to the double infection of BKD and *A. hydrophila*, they showed the greatest susceptibility to *V. anguillarum*. Ehlinger (1977) observed that certain selected brook trout strains, though resistant to furunculosis, were more susceptible to gill disease than was the native stock. Consequently selection of stocks for resistance to several diseases would be difficult (McIntyre 1977), except possibly when the pathogens are closely related (Hutt 1970).

Judging by the present results, it appears that the importance of transferrin genotypes in resistance to disease is stock specific. Differences among genotypes were only observed in the Alsea and B × S coho salmon infected with BKD. Weinberg (1974) noted that different host species may vary in the extent to which they rely on iron-specific nutritional immunity. Although only the most common genotypes were compared within each stock, it is unlikely that other genotypes would have shown greater resistance to BKD; their frequencies within the stocks would have been increased by natural selection if the disease plays an important role as a selective agent. However, it is apparent that factors other than disease may select for different transferrin genotypes. In Ukranian carp, *Cyprinus carpio*, general survival rates were highest among individuals with the AC genotype (Balakhnin and Galagan 1972). There is also an association of transferrin phenotype with weight gain in juvenile rainbow trout that may be due to the linkage of the transferrin locus with a gene or gene complex affecting growth (Reinitz 1977). The association of resistance to BKD with transferrin genotype may also be due to a gene linkage; if so, transferrin serves only as a marker. McIntyre and Johnson (1977) observed higher growth rates and better survival in AA than in AC transferrin genotypes of Big Creek coho salmon. While the frequency of the C allele is high in the Alsea stock, that frequency is depressed in a mixed population at Big Creek where Alsea coho salmon have been used to supplement the broodstock (J. D. McIntyre unpubl. data). Although BKD selects for the C allele in the Alsea coho salmon, the advantage of this allele is offset by some other more important selective factor, such as growth rate, within the Big Creek stock.

It is also conceivable that transferrin genotypes provide resistance to different diseases, or not at all—as with vibriosis. The ability to synthesize iron chelators—compounds necessary to remove iron from transferrin—is considered a virulence factor for certain pathogens (Arnold et al. 1977). Perhaps the iron chelators of *V. anguillarum* remove iron from transferrin more efficiently than do those of BKD bacteria. This more efficient removal would explain to some extent the lack of differential resistance to vibriosis among genotypes within both coho salmon and steelhead trout stocks. Pratschner (1978) observed differential resistance among transferrin phenotypes to vibriosis and several other diseases in coho salmon from the Skagit River, Wash. The AA phenotype exhibited greater susceptibility to vibriosis and cytophagosis but greater resistance to furunculosis while the CC phenotype was most resistant to vibriosis and very susceptible to furunculosis and cytophagosis. The disparity between Pratschner's and our results with respect to vibriosis may be due to the stock-specific nature of transferrin. Possibly differences among transferrin genotypes are more significant in a chronic disease such as BKD, and less so in an acute disease such as vibriosis—or perhaps the rapid death rate following exposure to *V. anguillarum* compressed the results too much to allow differences to be observed. Because of the short time span involved to vibriosis infections, the benefit of such differences to individual fish would be negligible.

Keeping in mind such considerations as selection for transferrin genotypes by different factors such as growth or disease, it becomes clear (as with stocks) that selectively breeding for certain transferrin genotypes would not be advisable. Though selection for one particular genotype might provide resistance to BKD, it might also entail lower growth rates or even greater susceptibility to other diseases. McIntyre (1977) cautiously recommended selective breeding for disease resistance only in propagated fish being held under

carefully controlled conditions or when one particular pathogen is a recurrent problem. Otherwise, it seems advisable to maintain variability in a stock to meet the demands of a variable environment.

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REMARKS ON SYSTEMATICS, DEVELOPMENT, AND DISTRIBUTION OF THE HATCHETFISH GENUS *STERNOPTYX* (PISCES, STOMIATOIDEI)

JULIAN BADCOCK[1] AND RONALD C. BAIRD[2]

ABSTRACT

Sternoptyx pseudodiaphana Borodulina is reported from the eastern North Atlantic in sympatry with *S. diaphana*, providing conclusive evidence that the former represents a species distinct from *S. diaphana*. Patterns of geographic variation among various characters are apparent in species of *Sternoptyx* as is allometric growth. These patterns render species identification difficult in certain allopatric populations, particularly those from the Atlantic and Pacific Oceans. Each species has distinct patterns of horizontal and vertical distribution and where species occur in sympatry, their centers of abundance do not coincide. Members of the genus *Sternoptyx* inhabit the "lower mesopelagic depth zone" (sensu Baird) from 500 to 1,500 m. Geographic variation in depth of maximum abundance for various species can be demonstrated. These appear correlated with variations in temperature and light although competitive interactions may also contribute to observed depth ranges. Photophore development is similar in the three species described and postlarval individuals of *S. diaphana* and *S. pseudodiaphana* are readily distinguishable. Characters useful in distinguishing the various species are presented in relation to patterns of geographic variation.

A single ancestral species which gave rise to the four presently recognized species, each exhibiting slight morphological divergence, is advanced as a parsimonious initial hypothesis of evolutionary relationship.

The genus *Sternoptyx* has, until recently, been thought to contain but a single polymorphic species (Schultz 1961, 1964). However, Baird (1971), and more recently Haruta and Kawaguchi (1976), have demonstrated the validity of three morphologically similar species, *S. diaphana* Hermann, *S. obscura* Garman, and *S. pseudobscura* Baird, each with broad but distinct geographic ranges. Baird (1971) also noted a morphologically distinct population of *S. diaphana* from the subtropical convergence region of the South Pacific. In view of the degree of character similarity and lack of sympatry with other populations of *S. diaphana*, he considered his data insufficient to substantiate the Southern Ocean form as a distinct species. Borodulina (1977) subsequently described the Southern Ocean form as *S. pseudodiaphana* and has recently published a synopsis of the hatchetfish genera *Argyropelecus* and *Sternoptyx* based on Russian collections (Borodulina 1978).

Sternoptyx pseudodiaphana from the eastern tropical Atlantic occurs in sympatry with *S. diaphana*. Our new data provide conclusive evidence that *S. pseudodiaphana* represents a species distinct from *S. diaphana*. Patterns of geographic variation are not well known in deep-sea fishes and patterns occur in the genus *Sternoptyx* which tend to obscure species distinctions among certain allopatric populations. Characters found useful in distinguishing among various species and populations are presented which complement and expand the treatments of Baird (1971) and Borodulina (1978). We describe metamorphic and postlarval development for various species and include comparisons among species. Additional data on the geographic and vertical distribution of the genus, including information from discrete-depth trawling studies, are presented which add considerably to our knowledge of the distribution of this widespread group of mesopelagic fishes.

METHODS

All four species of *Sternoptyx* were examined. The material and its sources are listed in Appendix Table 1. The specimens were fixed in Formalin[3] and preserved either in alcohol (70% ethyl or

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40% isopropyl) or in aqueous storage fluid (10% propylene glycol, 1% Formalin, 0.5% phenoxytol, based upon Steedman 1974). Generally, specimens were taken by various open midwater nets; however, a number of samples were taken with opening/closing nets of various designs (Clarke 1969; Baker et al. 1973; Hopkins et al. 1973).

Photophore Nomenclature

The unique pattern of photophore clustering in the family Sternoptychidae (sensu Baird 1971) has resulted in a different system of nomenclature from that used for other stomiatoid families (Figure 1). Weitzman (1974) suggested a revised nomenclature for stomiatoid taxa to include the hatchetfishes and for convenience, both appear in Table 1 (Weitzman's slightly modified). The distinct and unusual specializations in external morphology in the hatchetfishes (sensu Baird 1971) make determinations of homology among photophore groups difficult. We regard the new terms, therefore, as a convenience rather than as suggestions of homologies between similarly named photophore groups throughout the Stomiatoidei. For instance the preorbital photophore (PO) of the genus *Sternoptyx* differs from that of either *Argyropelecus* or *Polyipnus* morphologically, and probably functionally, and is perhaps more aptly termed an oral organ (Herring 1977). Nevertheless, for convenience, the term PO (ORB of Weitzman) is retained.

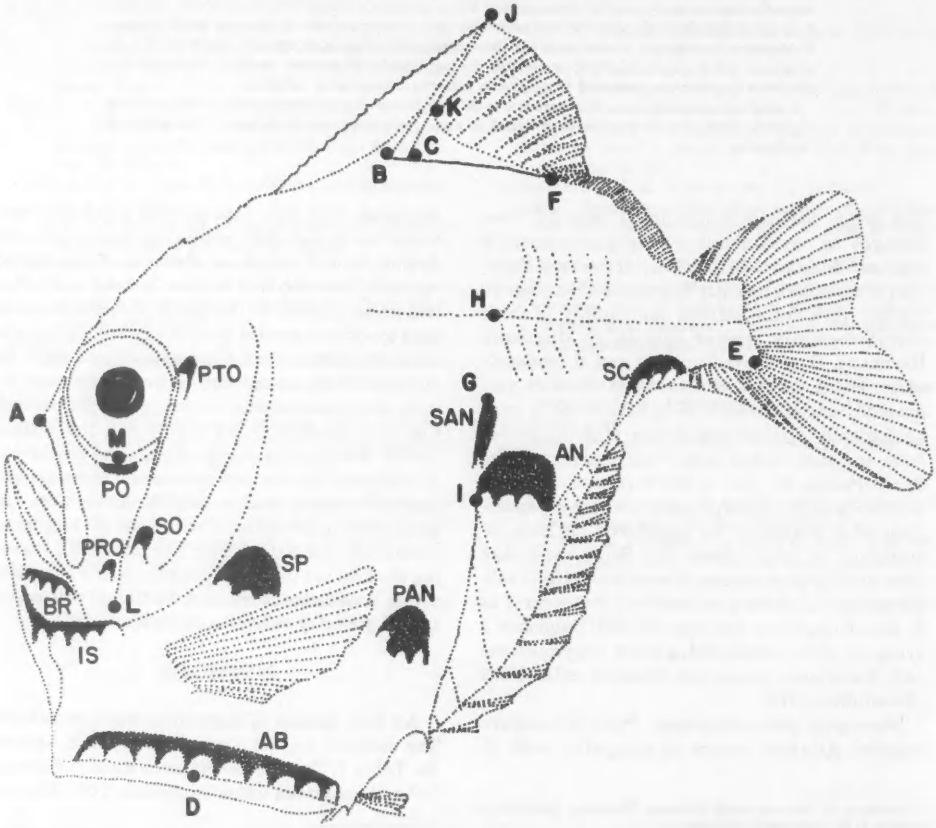

FIGURE 1.—Nomenclature of photophores and basic measurements for *Sternoptyx* spp.

TABLE 1.—Photophore development of *Sternoptyx pseudodiaphana* and *S. diaphana*, expressed in stages. Asterisk denotes earliest stage for photophore group completion; parentheses indicate photophore nomenclature in Baird 1971.

Stage	SL range (mm)	Number of photophores per photophore group (each size)												
		OP_3 (SO)	ORB (PO)	BR (BR)	PV (AB)	IP (I)	OV (SP)	OP_2 (PTO)	AN (AN)	VAV (PAN)	SC (SC)	OP_1 (PRO)	SAN (SAN)	No. of specimens
S. pseudodiaphana: eastern North Atlantic														
1	10.0-10.2	1*	1*	2	8	3-4	2	1*	0	0	0	0	0	2
2	8.3- 9.7	1	1	2	8- 9	4	3*	1	1	0	0	0	0	2
3	7.6- 9.2	1	1	2	8-10*	4	3	1	1	1	0	0	0	5
4	7.9-10.0	1	1	2	10	4-5*	3	1	2	1-2	1-2	0	0	14
5	9.8-10.5	1	1	3*	10	5	3	1	3*	3*	2	0	0	2
6	9.5-11.1	1	1	3	10	5	3	1	3	3	2-3	1*	0	13
7	11.2-14.1	1	1	3	10	5	3	1	3	3	3	1	1*	22
8	[1]13.0/[2]16.2	1	1	3	10	5	3	1	3	3	4*	1	1	
S. pseudodiaphana: southeastern Pacific														
2	6.5- 8.4	1	1	2	7- 8	4	3	1	1	0	0	0	0	3
4	7.6- 9.6	1	1	2	8-10*	4-5*	3	1	1-2	1-2	1-2	0	0	12
6	9.6- 9.9	1	1	3	10	5	3	1	3*	2-3*	1-2	1	0	2
7	9.7-14.3	1	1	3	10	5	3	1	3	3	2-3	1	1	7
S. diaphana: western North Atlantic														
2	7.0	1*	1*	2	8	4	3*	1*	1	0	0	0	0	1
3	7.0- 7.6	1	1	2	9-10*	4	3	1	1-2	1-2	0	0	0	7
4	7.6- 8.3	1	1	2	9-10	4-5*	3	1	2	2	1-2	0	0	4
5	7.8- 9.4	1	1	2-3*	10	5	3	1	2-3*	3*	2	0	0	6
6	8.8-10.5	1	1	3	10	5	3	1	2-3*	3*	2	1*	0	11
7	9.8-13.2	1	1	3	10	5	3	1	3	3	2-3	1	1*	22
8	[1]12.8/[2]13.6	1	1	3	10	5	3	1	3	3	4*	1	1	

[1]Smallest observed size.
[2]All specimens equal or larger have all photophores.

In this account, where reference to a particular photophore within a group is made, numbering is in an anteroposterior direction (e.g., AB(PV) 10 is the posteriormost photophore pair).

Measurements and Counts

The peculiar morphology of marine hatchetfishes has necessitated a number of modifications to measurements commonly used to describe teleost fishes. While most of those used here have been described by Baird (1971), it is difficult to precisely determine reference points in the genus *Sternoptyx*. All measurements used here are defined as the shortest distance between two stated points. Standard length (SL) in juveniles and adults was measured to the nearest 1 mm, but in postlarvae, to the nearest 0.1 mm. Other measurements of all specimens were taken to 0.1 mm. Measurements were as follows (letters refer to points on Figure 1):

Standard length (SL): from the tip of the snout (A) to the furthermost extension of the caudal peduncle (E);

Body depth: from the dorsal blade origin (B) to the midpoint of the ventral body margin (D);

SAN photophore depth: from the dorsalmost point (G) of the photophore SAN to the dorsal body margin (F) at the base of the posteriormost dorsal ray;

Midline height: from the anteroventral edge (I) of the photophore group AN to the trunk midline of horizontal septum (H) on a line passing through the photophore SAN;

SAN photophore height: from the anteroventral edge (I) of the photophore group AN to the dorsalmost point (G) of the photophore group SAN;

Trunk depth (TD): from the posterior end of the dorsal fin base (F) to the anteroventral edge (I) of the photophore group AN;

Trunk length: from the point of the trunk midline defined by the midline height measurement (H) to the posteriormost extent of the caudal peduncle (E);

Photophore lengths (AN and SC): the distance between the farthest extensions of the darkly pigmented photophore margins;

Dorsal fin base: from the origin of the first (K) to that of the last (F) dorsal ray;

Dorsal blade height: from the dorsal body margin (C) to the blade tip (J), along blade axis;

Orbital diameter: the length of the longest orbital axis (fleshy orbit);

Suborbital length: from the midventral point of the orbit (M) to the tip (L) of the preopercular spine.

It was not possible for one person to measure or take counts on all the specimens examined. The results obtained, however, were in good agreement, although it is inevitable that some variation

expressed may have been due to the individual measurer. All postlarval measurements and comparisons were made by one person (i.e., SL <18 mm). The postlarval phase was considered concluded at the attainment of a full complement of pigmented photophores (ca. 14-18 mm), at which stage individuals were classified as subadults. Meristic counts were made in accordance with Baird (1971) and vertebral counts included all separated vertebrae with the exception of the urostylar complex.

SYSTEMATIC REMARKS

Species Distinction

Morphological distinctions among species of *Sternoptyx* are relatively slight and distinctive characters tend to be obscured in allopatric populations, making identification difficult in the absence of other species. As an aid to the identification of specimens with a full complement of photophores (ca. 18 mm SL), the distinctive species characteristics reported by Baird (1971), Haruta and Kawaguchi (1976), and Borodulina (1978) are combined and expanded in relation to observed patterns of geographic variation. Characters used in distinguishing the four species are discussed below and each species is illustrated (Figures 2-5). Selected meristic and morphometric data are presented in Tables 2 and 3. Table 4 provides a synopsis of characters useful in differentiating adults and subadults.

The genus can be divided into two morphological groups or species pairs. In one, containing *S. pseudodiaphana* (Figure 2) and *S. diaphana* (Figure 3), the AN photophores completely fill the anal fin base, the horizontal part of the ventral body margin extends very little posterior to AN, and the posterior anal fin pterygiophores are relatively short. The second group, with *S. obscura* (Figure 4) and *S. pseudobscura* (Figure 5) is characterized by species having an appreciable extension of the horizontal part of the ventral body margin posterior to AN, long posterior anal fin pterygiophores, and smaller AN and SC (Table 3).

Within these two groups, species may be readily separated from one another, albeit more through a combination of characters than by virtue of a single one. *Sternoptyx pseudodiaphana* and *S.*

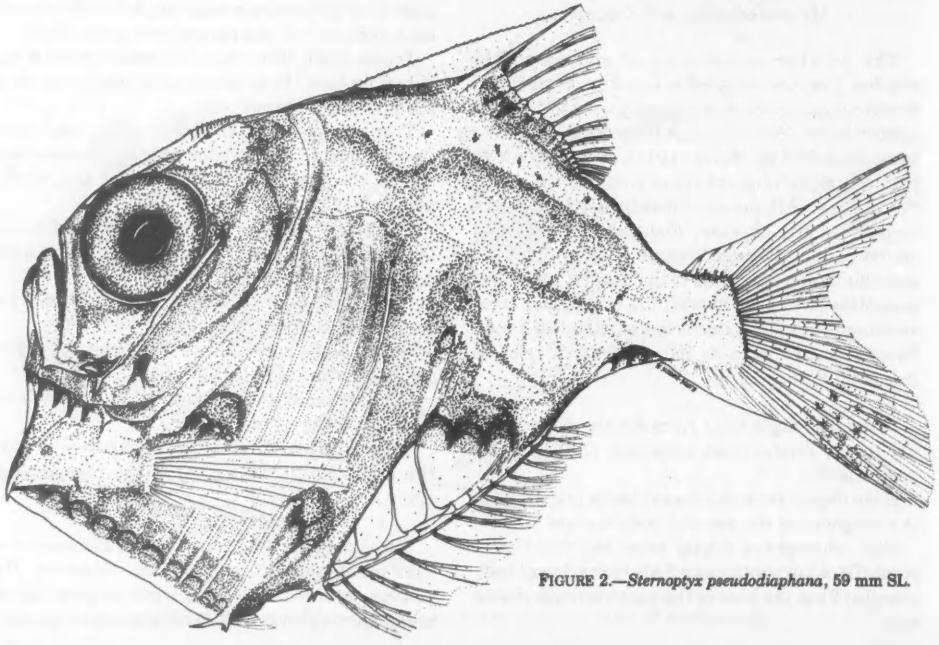

FIGURE 2.—*Sternoptyx pseudodiaphana*, 59 mm SL.

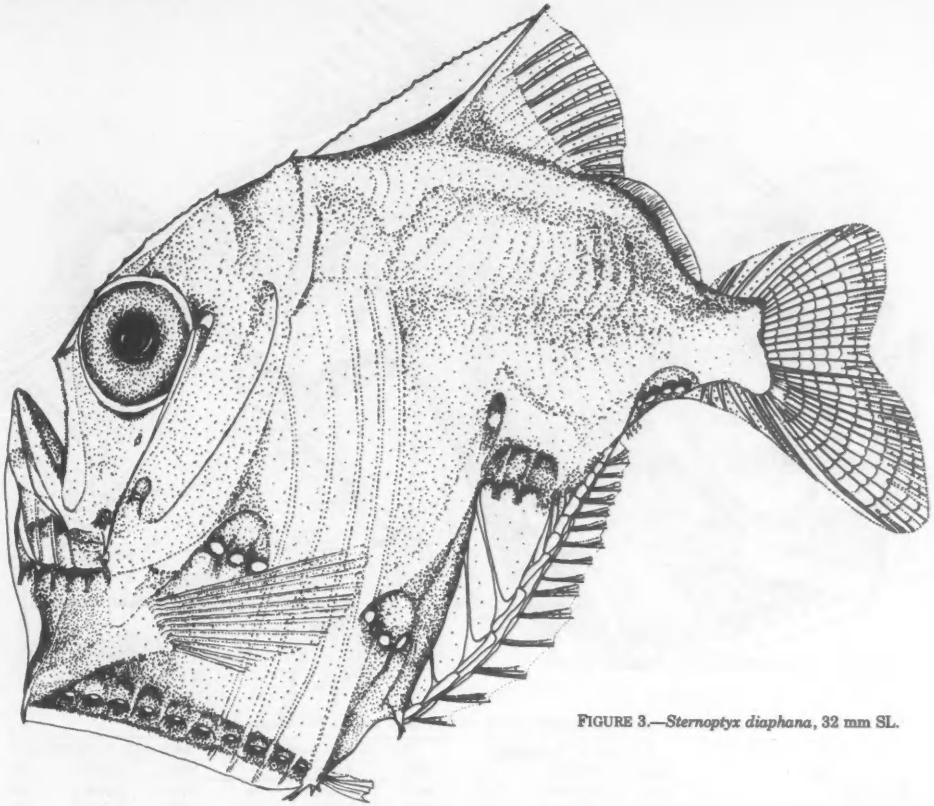

FIGURE 3.—*Sternoptyx diaphana*, 32 mm SL.

TABLE 2.—Meristic counts of *Sternoptyx* species.

Species	Vertebral no.						Dorsal rays					Anal rays					Gill rakers (1st arch)			
	27	28	29	30	31	32	9	10	11	12	13	12	13	14	15	16	6	7	8	9
S. diaphana[1]	2	30	12	—	—	—	7	7	3	—	—	—	2	9	4	—	2	39	3	—
S. pseudobscura[2]	1	8	19	1	—	—	3	4	3	—	—	—	3	5	2	—	—	18	34	3
S. obscura[3]	—	—	2	8	—	—	3	5	1	—	—	3	7	—	—	—	—	9	4	3
S. pseudodiaphana[4]	—	—	4	40	53	8	4	11	54	53	4	—	1	21	5	1	2	68	11	—
S. pseudodiaphana[5]	—	—	3	20	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
S. pseudodiaphana[6]	—	—	—	1	21	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—

[1]Atlantic and Pacific populations represented.
[2]Atlantic and central Pacific populations represented.
[3]East Pacific populations only.
[4]Northeastern and southern Atlantic and southeastern Pacific populations represented.
[5]Tropical Atlantic subset (included in 4).
[6]Southeastern Pacific subset (included in 4).

diaphana (>18 mm SL) can be distinguished on the basis of vertebral number 29-32 versus 27-29, respectively, Table 2; see also Borodulina 1978), and the placement of the photophore SAN (described by SAN depth/SL and trunk depth/SAN height, Figures 6, 7) which is appreciably raised in *S. pseudodiaphana*. Overlap of more than one of these three characters in any given specimen was rarely observed. Other differences, most noticeable in sympatric populations, occur in body shape and pigmentation. *Sternoptyx diaphana* is generally deeper in body and especially trunk, appreciably less pigmented, and lacks streaks on the outer ventral caudal fin margin in larger individuals (Tables 3, 4).

Sternoptyx obscura is distinguished from *S.*

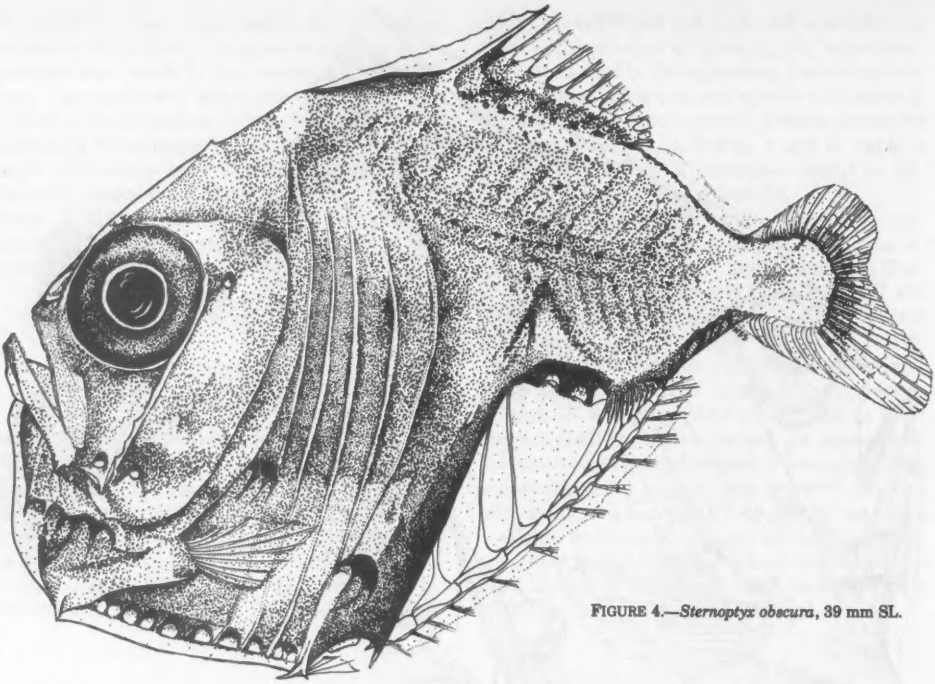

FIGURE 4.—*Sternoptyx obscura*, 39 mm SL.

TABLE 3.—Proportional measurements of *Sternoptyx* species for various size classes.

Item	11-16 mm SL[1] *S. diaphana*			17-47 mm SL *S. diaphana*			16-55 mm SL *S. pseudobscura*		
	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
Body depth[2]	85.2	80.8-90.0	7	87.1	75.7-96.7	74	87.4	73.2-96.2	52
AN length[2]	10.1	8.2-11.4	11	12.0	9.4-13.9	58	8.6	5.5-10.5	45
SC length[2]	5.5	4.2-6.4	8	7.3	5.9-11.2	55	5.3	3.8-6.7	41
SAN depth[2]	29.8	28.3-31.8	10	33.2	27.0-39.7	88	20.8	14.4-30.7	66
Trunk depth[2]	38.0	34.2.40.8	11	44.1	38.3-49.5	88	39.5	33.7-46.7	56
Trunk length[2]	36.1	34.2-38.2	11	36.1	32.0-43.8	86	35.6	27.0-41.5	54
Trunk depth/trunk length	1.05	1.00-1.12	11	1.21	0.94-1.37	86	1.12	0.95-1.33	54
Dorsal base/dorsal blade	—	—	—	0.76	0.56-1.00	72	0.79	0.56-0.94	19
Trunk depth/SAN height	4.4	3.8-6.0	11	3.8	2.9-6.1	86	2.0	1.6-2.5	56
Orbit diameter/suborbital length	0.89	0.83-0.95	11	1.03	0.89-1.21	57	0.85	0.72-1.04	37
Item	13-17 mm SL[1] *S. pseudodiaphana*			18-61 mm SL *S. pseudodiaphana*			15-40 mm SL *S. obscura*		
	Mean	Range	*n*	Mean	Range	*n*	Mean	Range	*n*
Body depth[2]	78.6	70.1-89.4	27	80.8	70.5-92.6	131	74.9	68.4-82.1	18
AN length[2]	9.8	7.6-11.8	36	11.4	8.8-13.7	120	8.5	6.0-11.1	11
SC length[2]	6.3	5.3-7.6	19	7.6	5.0-11.7	120	5.1	4.0-7.7	11
SAN depth[2]	24.4	22.3-31.8	36	25.3	21.7-33.2	132	22.9	20.3-26.2	18
Trunk depth[2]	35.8	31.4-41.2	36	38.8	33.5-46.6	132	31.6	27.5-35.1	18
Trunk length[2]	37.4	32.9-43.8	36	37.7	33.2-43.4	132	37.7	32.5-42.2	18
Trunk depth/trunk length	0.95	0.83-1.11	34	1.03	0.86-1.24	131	0.83	0.75-0.94	26
Dorsal base/dorsal blade	—	—	—	0.90	0.65-1.12	51	1.14	1.03-1.43	14
Trunk depth/SAN height	2.8	2.3-3.4	32	2.7	2.1-3.4	132	3.6	2.6-5.1	18
Orbit diameter/suborbital length	1.06	0.96-1.21	36	1.07	0.92-1.45	108	1.05	0.89-1.30	10

[1]Subadults.
[2]Percent standard length.

pseudobscura (and indeed, all other species of *Sternoptyx*) by the narrow shape and configuration of the trunk and also the high dorsal fin base/dorsal blade ratio. The trunk is markedly longer than it is deep, while the dorsal blade height is usually much shorter than dorsal fin base length

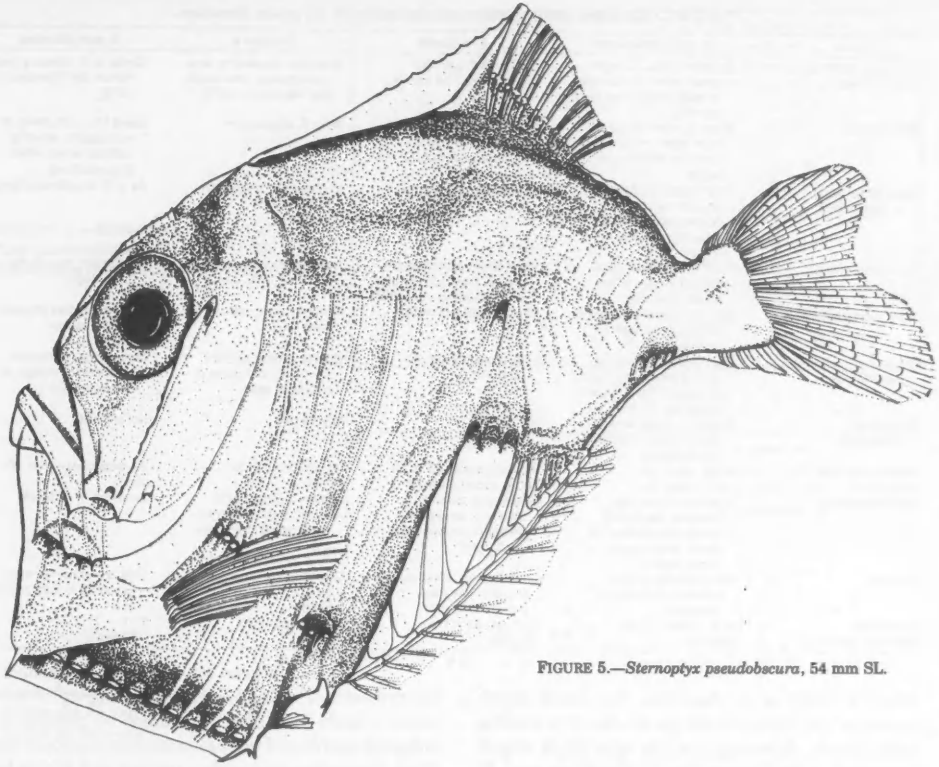

FIGURE 5.—*Sternoptyx pseudobscura*, 54 mm SL.

(Table 3). *Sternoptyx obscura* is further distinguished from *S. pseudobscura* by its lower placement of the photophore SAN and by uniformly dark pigment of body and trunk, as well as the presence of a dark corona along the caudal fin rays, radiating from the fin base.

Geographic Variation

The degree of genetic differentiation and nature of geographic variation in populations of midwater fishes have not been thoroughly explored, though evidence is now accumulating that such variation does exist and may be widespread in species with broad geographic ranges (e.g., Naftaktitis 1968; Baird 1971; Pertseva-Ostroumova 1974; Karnella and Gibbs 1977). Baird (1971) was able to distinguish separate populations in several species of the related hatchetfish genus *Argyropelecus*. Populations tended to remain distinct over time and differences among populations were generally associated with zoogeographic boundaries. The present evidence indicates that similar patterns of geographic variation occur in species of *Sternoptyx*, the extent of which awaits more extensive investigation.

Geographic variation is apparent in both *S. pseudobscura* and *S. pseudodiaphana*. The systematic problems arising from such variation are illustrated in Figures 6 and 7. In addition to the indicated allometry, the suitability of the two character complexes (trunk depth/SAN photophore height and SAN photophore depth) for distinguishing species differs, depending on the populations being compared. Both characters are distinctive among the three species illustrated (*S. diaphana, S. pseudodiaphana,* and *S. pseudobscura*) for sympatric populations in the North Atlantic. However, where southeast Pacific populations of *S. pseudodiaphana* are compared with

TABLE 4.—Characters useful in differentiating species of the genus *Sternoptyx*.

Character	*S. pseudodiaphana*	*S. diaphana*	*S. obscura*	*S. pseudobscura*
Anal pterygiophore configuration	No appreciable pterygiophore extension posterior to anal photophores (>18 mm SL)	Similar to *S. pseudodiaphana* (>18 mm SL)	Extension posterior to anal photophores (see Haruta and Kawaguchi 1976)	Similar to *S. obscura* (see Haruta and Kawaguchi 1976)
SAN position	About 3 or less times in trunk depth; not more than 3½ times in subadults	More than 3 times in trunk depth: more than 4 times in subadults (<ca. 17 mm)	As in *S. diaphana*	About 1½ to 2½ times in trunk depth; raised to midtrunk line in Atlantic populations
Ratio dorsal base to dorsal blade	Dorsal base normally shorter than blade, occasionally about equal to or slightly longer	Dorsal base usually less than 0.9 of blade	Dorsal base longer than dorsal blade	As in *S. pseudodiaphana*
Trunk dimensions	Trunk depth about equal to trunk length; in subadults often less	Trunk depth conspicuously greater than trunk length; in subadults can be equal	Trunk depth conspicuously less than trunk length	Trunk width greater than trunk length
Trunk pigmentation	Dark bar above midline, little pigment near midline	Light in region of midline	Uniformly dark over whole trunk region	Nonuniform dark pigment in trunk region
Caudal fin pigmentation	Light pigment streaks at ventral outermost margin of caudal rays of larger adults (ca. 40 mm)	Little or no pigment on caudal rays	Corona of dark pigment spreading from base of caudal fin rays	Dark pigment restricted to innermost margin of caudal fin rays
Pectoral fin pigmentation	Absent in adults; present at ray bases in juveniles and subadults	Not present	Not present	Not present
Vertebral number	30-32, rarely 29	28, occasionally 27 or 29	30, occasionally 29	29, ocasionally 28 or 30
Anal rays	14-15, rarely 13	14-15, occasionally 13	12-13	13-15
Anal photophores	In adults: longer than peduncle depth; little horizontal extension of ventral body margin above anal fin	Similar to *S. pseudodiaphana*; anal photophores fill pterygiophore "gap"	Shorter than peduncle depth; body margin extends posteriorly above anal fin	Similar to *S. obscura*
Eye size	Orbit diameter greater than suborbital length; rarely less	Orbit diameter about equal to, often less than, suborbital length	Orbit diameter usually greater than suborbital length	Orbit diameter less than suborbital length, equal to it
Dorsal rays	9-13, usually 11-12	9-11, usually <11	9-11, usually <11	9-11
Maximum size (SL)	>60 mm	<50 mm	<45 mm	>55 mm

Atlantic forms of *S. diaphana* the trunk depth character exhibits overlap particularly in smaller individuals. Likewise, while the SAN depth character is distinctive for *S. diaphana* and *S. pseudodiaphana*, there is considerable overlap when Pacific populations of *S. pseudobscura* are compared with *S. pseudodiaphana*. The lower position of the SAN photophore has been illustrated by Haruta and Kawaguchi (1976, figure 6) for western Pacific forms of *S. pseudobscura* and can be compared with the Atlantic form illustrated here (Figure 5). Differences in vertebral number between Pacific and tropical Atlantic forms of *S. pseudodiaphana* are indicated (Table 2) and the character should be useful in distinguishing the Pacific population from *S. obscura*.

Postlarval Development

Characters useful in distinguishing later life stages are often less suitable or ineffective for metamorphosing and postlarval stages or indeed small (<18 mm) subadults. Geographic variation and allometric growth further complicate identification. The present data, while substantiating the presence of both allometry and geographic variation (Table 3; Figure 7), cannot be considered comprehensive and intensive studies of collections from numerous geographic regions are yet to be done. The extension of the ventral trunk margin, size of AN photophore group, and elongate posterior pterygiophores appear to be neotenic characters established from mid- to late-metamorphic stages (Figures 8, 9) and are consequently less useful as species-distinctive characters for early life stages.

When present, the location of photophore SAN is diagnostic, though the placement tends to be somewhat lower on the body in postlarvae. SAN is closely associated with photophores AN in *S. diaphana* and not markedly raised in *S. obscura*. For *S. pseudodiaphana* and *S. pseudobscura* it is vertically separated from the AN group. In Atlantic populations of *S. pseudobscura* the photophore SAN is raised to the midtrunk line, distinguishing it from other congeners. The lower SAN position in Indo-Pacific populations of *S. pseudobscura* make this character less useful in separating it from *S. pseudodiaphana*. The smaller eye (noted by Günther 1887) in *S. pseudobscura* (Table 3) is

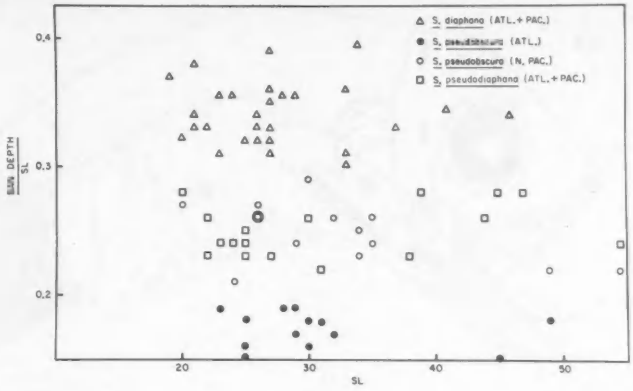

FIGURE 6.—Scattergram of ratio of SAN photophore depth/SL and SL (millimeters) for three species of *Sternoptyx*.

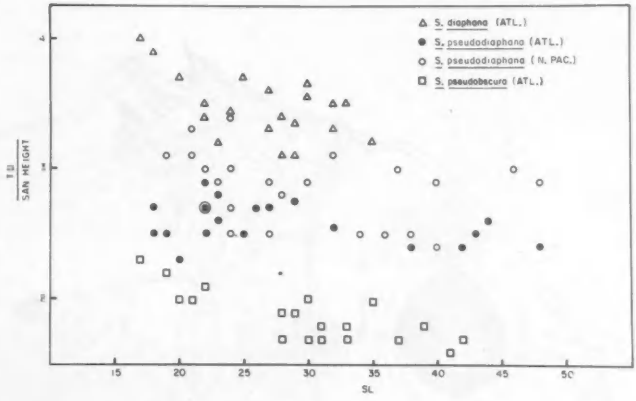

FIGURE 7.—Scattergram of ratio of trunk depth (TD)/SAN photophore height and SL (millimeters) for three species of *Sternoptyx*.

diagnostic while small individuals of the two species may be separated on the basis of pectoral fin ray pigment present in *S. pseudodiaphana*. The young of *S. obscura* are uniformly pigmented and have the characteristically narrow trunk at quite small sizes.

The sequence of numbered "stages" in which photophore groups appear and are completed is listed in Table 1 for *S. pseudodiaphana* and *S. diaphana*. The sequential pattern is identical in both species, and limited data suggest *S. pseudobscura* also conforms to this pattern though the early-metamorphic forms of these species are as yet undescribed. For ease of reference a sequence of stages based on the order of appearance of photophores during development is presented in Table 1. The brief account given below is intended primarily to outline the major anatomical landmarks during metamorphosis and to indicate some of the distinctions among species during postlarval development.

Sternoptyx pseudodiaphana

The least developed specimen observed of *S. pseudodiaphana* from the Atlantic (10.2 mm SL) is elongate, with the head about 25% of SL. Dorsal and pelvic fins are undeveloped, while the pectoral fin has six and the anal seven rays developing. The caudal has 19 rays. The postlarva is relatively transparent and pigment is restricted to certain areas: a symphysial pair of spots, two isthmus spots, the pectoral fin, and a caudal peduncle spot. Internally, the swim bladder is pigmented dorsad, as is the posterior part of the stomach. Meningeal pigment is present both as a melanophore in the

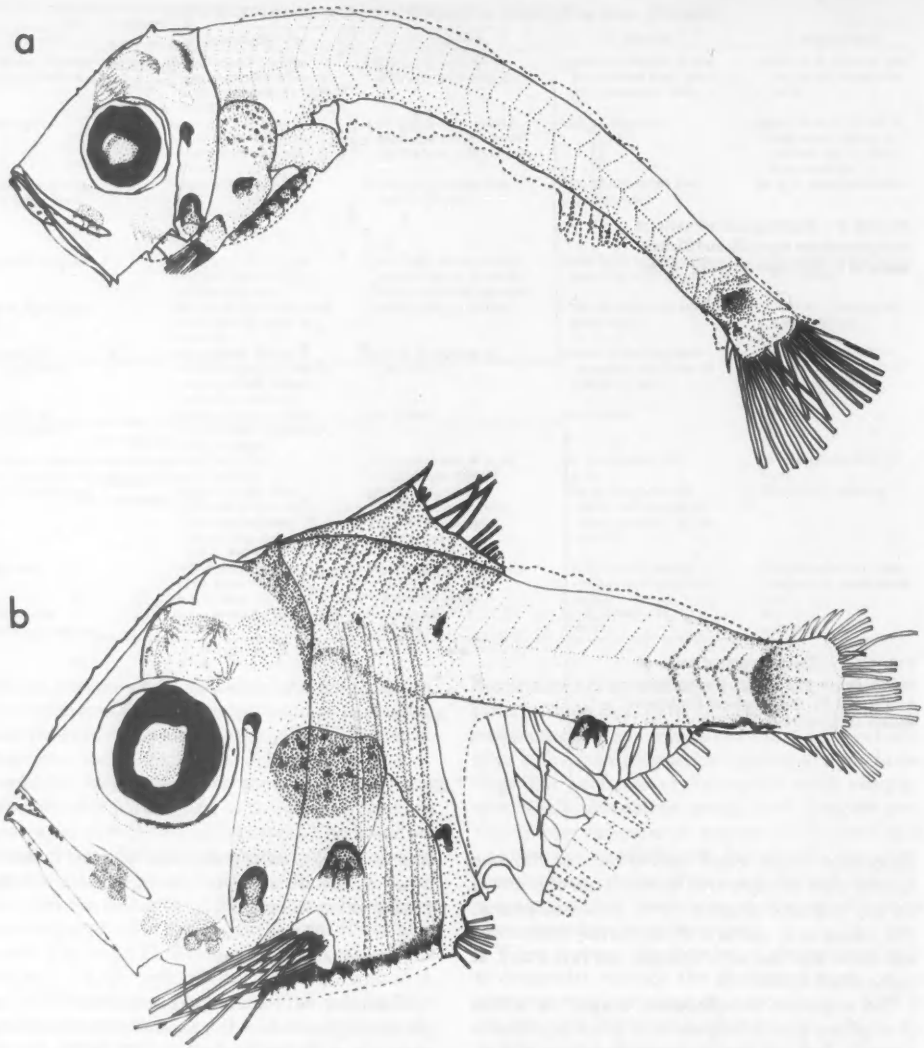

FIGURE 8.—Development of *Sternoptyx pseudodiaphana*: (a) Stage 1, 10.0 mm SL; (b) Stage 4, 8.9 mm SL.

pineal region and as scattered melanophores posterior to it. In the most advanced Stage 1 specimen (Figure 8a) additional pigment occurs anterior to the stomach. Stomach pigmentation is completed by Stage 3 and during this stage new pigment sites develop along the ventral margin of the orbit, in the opercular region, and along the predorsal crest. Light abdominal pigmentation appears during Stage 4 and the caudal pigment extends anteriorly along the dorsum (Figure 8b), reaching the dorsal fin base later in this stage. As development progresses, pigmentation spreads and intensifies

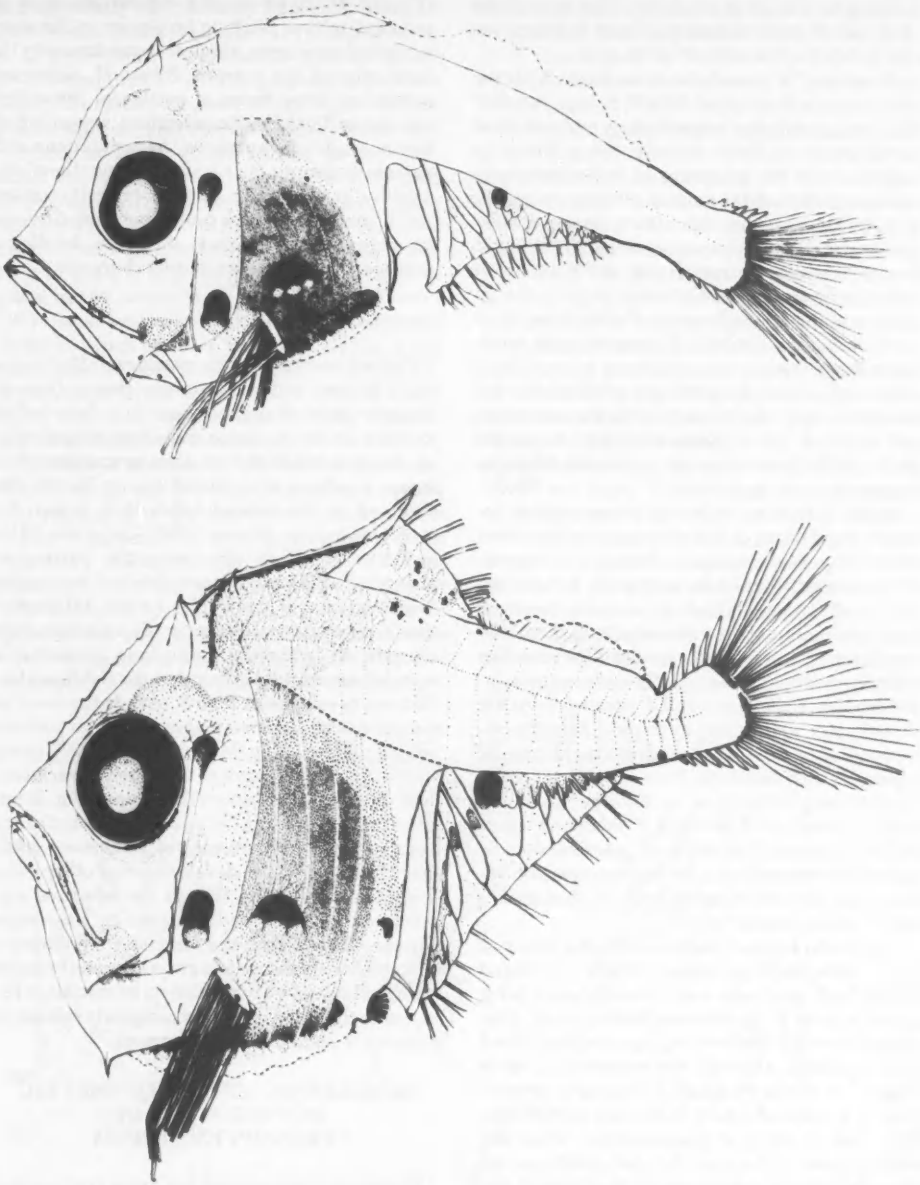

FIGURE 9.—Development of *Sternoptyx diaphana*: (upper) Stage 2, 7.0 mm SL; (lower) Stage 3, 7.2 mm SL.

leading to the adult condition. The rays of the dorsal fin first develop during Stage 3; the rays of the pelvic fin first appear in Stage 4.

A series of *S. pseudodiaphana* taken from the southeastern Pacific (lat. 33°-39° S, long. 80°-120° W) show a similarity in morphology and pattern of development to North Atlantic forms. The data indicate that the sequences of both appearance and completion of the various photophore groups are similar, although the relative timing of completion for certain groups may differ slightly. For example, while the completion of PV in North Atlantic forms apparently occurs prior to the initiation of SC, in southeastern Pacific forms it occurs afterwards (Table 1). Pigmentation in specimens from these two populations is essentially alike, but a small pigment spot located near the posterior end of the dentary in Pacific forms was not noted in the Atlantic material. As in the adults, differences between postlarvae from the two areas, then, does occur.

Slight differences in larval characteristics between populations of the same species have been shown for certain lanternfishes (Pertseva-Ostroumova 1974) and do occur in the genus *Sternoptyx*, differences which we suspect, based on *Argyropelecus*, may be more extensive than indicated here. They can render species differentiation difficult in certain areas. Early-metamorphic individuals of *S. diaphana* and *S. pseudobscura* are superficially similar and in tropical Atlantic collections only late-metamorphic stages can be separated with certainty. Metamorphic individuals of *S. pseudodiaphana*, on the other hand, are highly distinctive. A series of *S. diaphana* taken off Bermuda, an area where *S. pseudobscura* is apparently rare, allowed for some comparison between the midmetamorphic forms of this species and *S. pseudodiaphana*.

The caudal spot so conspicuous in the young of *S. pseudodiaphana* at Stage 1 (Table 1) is found neither in *S. diaphana* nor *S. pseudobscura* prior to completion of photophore development. Pigmentation of the pectoral fin rays has been found in *S. diaphana*, although not consistently, up to Stage 3. At any given stage, *S. diaphana* appears to be in a more advanced state both morphologically and in terms of pigmentation. Thus the configuration of the anal fin pterygiophores attains the juvenile appearance during Stage 3, appearing in Stage 4 in *S. pseudodiaphana*; the pelvic fins differentiate earlier (Stage 3 versus 4), as does the pigmentation of *S. diaphana* in general (Figure 9). Even so, the pigmentation of *S. pseudodiaphana* tends to be denser in the more advanced specimens, which are conspicuous by the dark color of the dorsum. Elbert H. Ahlstrom[4] recognizes three forms of postlarval *Sternoptyx* spp. in his North Pacific collections, none of which bear a caudal melanophore. As populations of *S. pseudodiaphana* are unknown north of the Equator in the Pacific, then, tentatively, postlarval *S. obscura* also lack caudal pigment. *Sternoptyx pseudodiaphana* may, therefore, be distinguished from congeners by this character.

General Comments

During metamorphosis postlarval *Sternoptyx* (ca. 6-14 mm) undergo extensive change from an elongate premetamorphic form to a deep-bodied juvenile. In earlier stages, metamorphic individuals are somewhat shorter than premetamorphic forms, a pattern of apparent loss in length also observed in the related hatchetfish genus *Argyropelecus* (e.g., Brauer 1906; Jespersen 1915; and others). While the sequential pattern of photophore addition appears identical among the species examined, timetables for the differentiation of other external characters do not necessarily coincide. As indicated, *S. diaphana* appears in a more advanced state of morphological differentiation and development than *S. pseudodiaphana* at comparable photophore stages. A similar pattern has been observed by Baird (unpubl. data) among species of *Argyropelecus*. Geographic variation both among and within species is apparent. It appears that there can be appreciable flexibility among species in the timing of photophore addition in relation to the development of other morphological characters, though the adaptive significance of these observations is presently unclear. Growth rate, the functional significance of photophore presence at a given size, and broader ecological considerations such as predation or resource availability, are likely complexly related to patterns of photophore development.

GEOGRAPHIC AND BATHYMETRIC DISTRIBUTION OF *STERNOPTYX* SPECIES

The genus is widespread, occurring in all oceans

[4]E. H. Ahlstrom, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. November 1975.

and apparently excluded only from polar seas and the Mediterranean (Jespersen 1915; Geistdoerfer et al. 1970; Baird 1971; Haruta and Kawaguchi 1976; Borodulina 1978). The geographic distributions of the species are presented in Figures 10 and 11 and, when coupled with the recent Russian data (Borodulina 1978), exhibit certain distinct patterns. The species tend to be limited to areas with hydrographically similar characteristics (sensu Baird 1971) and often exhibit mutually exclusive distributions. The horizontal distributions conform in general to zoogeographically distinct regions in the oceans (e.g., Baird 1971; McGowan 1977; Backus and Craddock 1977), the nature and limits of which are only generally defined. From the limited number of observations of vertical distribution in areas of sympatry, species which share the water column tend to have separate depths of maximum abundance.

Sternoptyx obscura is confined to the Indo-Pacific. In the eastern Pacific and Indian equatorial regions, it is the sole representative of the genus. In the periphery of its distribution, it can be relatively abundant (e.g., basins off southern California) and can occur in sympatry with *S. diaphana* and *S. pseudobscura* (Figures 10, 11). In general the geographic distribution resembles that of a number of other species, e.g., *Myctophum aurolanternatum, Cyclothone acclinidens, Scopelarchoides signifer, Rosenblattichthys alatus* (Nafpaktitis and Nafpaktitis 1969; Parin et al. 1973; Johnson 1974; Mukhacheva 1974; Quero 1974; Becker and Borodulina 1976), that are apparent equatorial Indo-Pacific endemics.

Sternoptyx diaphana and *S. pseudobscura* occur in the Atlantic and Indo-Pacific and overlap for much of their ranges (Figures 10, 11). *Sternoptyx pseudobscura*, however, is apparently uncommon in the western North Atlantic and the Caribbean, where *S. diaphana* is abundant, yet it is well represented in the Gulf of Mexico. The occurrence of all three species in Indonesian basin regions is indicative of the zoogeographic complexity of the mesopelagic ichthyofauna of that area.

Sternoptyx pseudodiaphana is widely distributed in the Southern Ocean (see also Borodulina 1978) and associated boundary currents in the Southern Hemisphere (Figure 11). Evidence from other studies (e.g., Alvarino 1965; Gibbs 1968; Krefft and Parin 1972; Nafpaktitis 1973; Mayer 1975; Bertelsen et al. 1976) has indicated that the subtropical convergence area, at least in the South Pacific, is a distinct zoogeographic region with a number of endemic or characteristic species. The occurrence of *S. pseudodiaphana* off South Australia, in the Indian Ocean, and across the South Atlantic between lat. 32°-40° S reinforces the concept that many elements of the subtropical con-

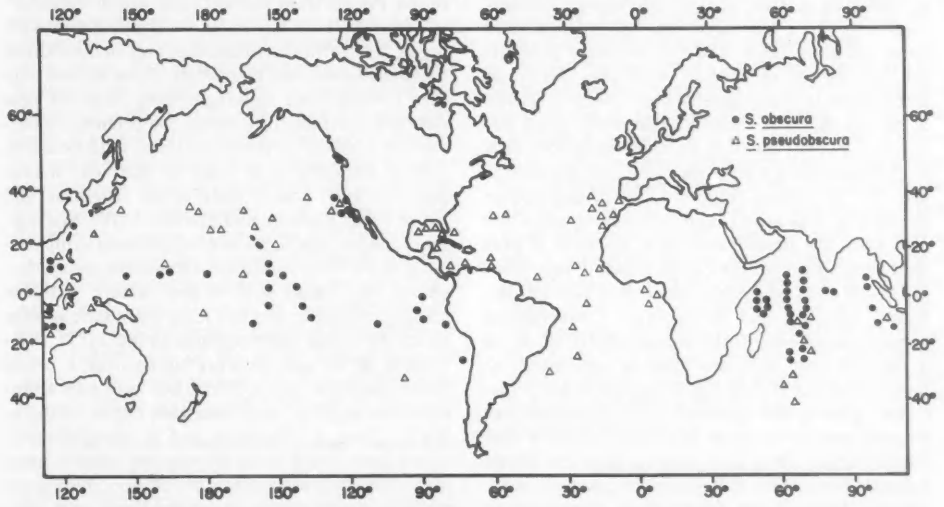

FIGURE 10.—Distribution of *Sternoptyx obscura* and *S. pseudobscura* (also from Baird 1971; Haruta and Kawaguchi 1976).

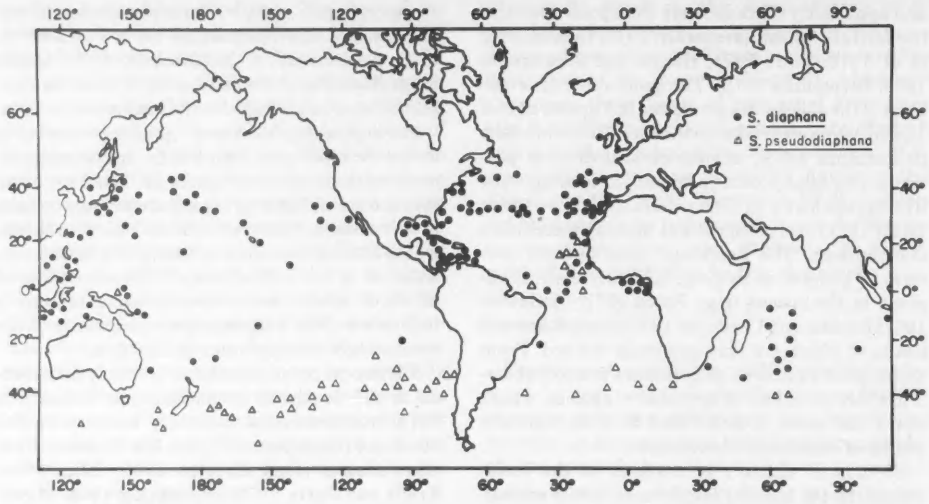

FIGURE 11.—Distribution of *Sternoptyx diaphana* and *S. pseudodiaphana* (also from Baird 1971; Haruta and Kawaguchi 1976).

vergence fauna in the Pacific have circum-Southern Ocean distributions (Craddock and Mead 1970). McGinnis (1974) has presented evidence in support of counterclockwise circulation in the Pacific subantarctic with observed endemism in mesopelagic fishes resulting from zoogeographic isolation of that region. *Sternoptyx pseudodiaphana* from this area can be distinguished from Atlantic forms and the evidence presented here is not in conflict with the McGinnis hypothesis. In the tropical eastern North Atlantic *S. pseudodiaphana* extends as far north as lat. 20° N, long. 21° W (where it exists in sympatry with *S. diaphana*) and it is not unlikely that it occurs in the Gulf of Guinea (Figure 11). Although some specimens have been taken in the Benguela Current area, the general paucity of material at present available from the South Atlantic precludes judgment as to whether a link exists between the North Atlantic and Subtropical Convergence populations. A potentially disjunct distribution, in a manner less extreme than is expressed by *Stomias boa boa* (Gibbs 1969), is given some tentative support by the apparent differences observed between postlarvae from the North Atlantic and South Pacific. Thus it is possible that the North Atlantic population of *S. pseudodiaphana* is a diverging form of the Subtropical Convergence stock. Finally, mention should be made of the single specimen apparently caught near the Philippines. There is no obvious mistake in the station labelling for this individual (*Challenger* Stn. 218). The species range extends considerably northward in the Atlantic and future studies may also confirm a more complex distribution pattern in the Pacific than present data would indicate.

The species of *Sternoptyx* are the deepest dwelling of the marine hatchetfishes and do not exhibit marked diel vertical migration. There are few capture records from opening/closing nets but new data are provided from recent comprehensive surveys (0-2,000 m) at three locations, in the eastern North Atlantic and Gulf of Mexico, where discrete-depth trawls were taken (Hopkins and Baird 1973; Badcock and Merrett 1976). *Sternoptyx diaphana* and *S. pseudobscura* occur sympatrically at all three locations. *Sternoptyx pseudodiaphana* was found only at the eastern Atlantic stations where it was the least abundant species at lat. 18° N but more common at lat. 11° N. Individuals of all species were taken over a broad depth range (ca. 500-2,000 m) but were only abundant over a much more restricted depth zone (Table 5). Thus, *S. diaphana* and *S. pseudobscura*, which have broad areas of sympatry, tend to have distinctly separate zones of maximum abundance while *S. pseudodiaphana*, at the limits of its distribution, is somewhat intermediate and overlaps

TABLE 5.—Range of depths of maximum abundance of species of *Sternoptyx* in sympatry at three locations (subadults and adults) (Hopkins and Baird 1973; Badcock and Merrett 1976).

Species	Lat. 27° N, long. 86° W	Lat. 18° N, long. 25° W	Lat. 11° N, long. 20° W
S. diaphana	600-750 m	600-800 m	500-700 m
S. pseudobscura	850-1,000 m	800-1,500 m	800-1,000 m
S. pseudodiaphana	Not present	600-1,500 m	600-1,000 m

both congeners (Table 5). The shoaling of *Sternoptyx* spp. between lat. 18° N and 11° N is not a function of developmental state and is a feature shown by many species of midwater fishes (Badcock and Merrett 1977).

In other areas of the eastern North Atlantic and also in the Gulf of Mexico where *S. pseudobscura* and *S. diaphana* share the water column, populations of *S. pseudobscura* are always centered below those of *S. diaphana*. Data presented by Baird (1971) indicated that *S. pseudodiaphana* is usually taken in 800-1,200 m depth in the Southern Ocean. Evidence from recent collections from the South Atlantic imply a similar pattern of vertical distribution.[5] In general, then, *S. pseudodiaphana* and *S. pseudobscura* may be regarded as deeper dwelling species of *Sternoptyx* while *S. diaphana* is a shallower living form. In certain areas of the Atlantic, discrete sampling has shown *S. diaphana* to be centered deeper than indicated above (Badcock 1970; Badcock and Merrett 1976; Roper et al.[6]). *Sternoptyx pseudobscura* has been shown to be of low abundance in these areas but the deepening of *S. diaphana* is likely to be a consequence of the sinking of isotherms relative to other areas. The role of competitive interactions among these species is yet undocumented and these may also exert an effect on geographic patterns of vertical distribution. Data on *S. obscura* are not comprehensive, but a preliminary survey of maximum depth of open trawl collections indicate a depth range similar to *S. diaphana* (500-1,000 m) in basins off southern California.

An analysis of the vertical distribution of mid- and late-metamorphic stages in the eastern North Atlantic was possible only for *S. pseudodiaphana* because of the problems in distinguishing between such individuals of the other two species examined. As with subadults and adults, individuals of like developmental stage lay shallower in the water column at lat. 11° N, long. 20° W than at lat. 18° N, long. 25° W (400-800 m versus 500-900 m depth). Although the data are sparse, there is evidence for ontogenetic vertical stratification among metamorphic stages. At lat. 11° N, long. 20° W, Stages 1-3 occurred only in 400-500 m depth; Stage 4 in 400-600 m; Stage 5 in 500-700 m; and Stage 6 in 500-800 m. A similar relationship is implied for metamorphic stages from lat. 18° N, long. 25° W, although stratification occurred deeper in the water column.

[5]G. Krefft, Institut für Seefischerei, Hamburg, West Germany, pers. commun. 1976.

[6]Roper, C. F. E., R. H. Gibbs, Jr., and W. Aron. 1970. Ocean acre: an interim report. Report to the U.S. Navy Underwater Sound Laboratory. Contract No. N00140-69-C-0166. Smithson. Inst., Wash., D.C., 22 p.

CONCLUSIONS

The evidence presented shows *Sternoptyx* to contain four closely related species. Morphological distinctions between them are relatively slight, but are consistent among the populations examined. The four species have broad geographic ranges and the limited data indicate the occurrence of geographic variation in *S. pseudobscura* and *S. pseudodiaphana* at adult and postlarval levels. Thus systematic difficulties arise in that certain characters useful in distinguishing species in sympatry may overlap when measurements from other populations are included.

Characters subject to allometric growth similarly present systematic problems. Nevertheless, most of the morphological criteria used here to separate species are maintained irrespective of population or developmental state. When found in sympatry, distinctions are clear and species consistently separable by many characters.

While we distinguish two species pairs on the basis of anal fin pterygiophore configuration, no hypothesis of cladistic relationship among the species is advanced. Considering the highly specialized and peculiar morphology of the genus (Baird 1971; Baird and Eckhardt 1972; Weitzman 1974; for discussion of family relationships), the most parsimonious hypothesis advanced is that a single ancestral species evolved which diverged considerably from a more generalized hatchetfish stock. Subsequent speciation in the genus probably involved the isolation of populations which now show very slight morphological divergence, exhibit various degrees of geographic variation, and have distinct horizontal and vertical patterns of distribution.

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APPENDIX TABLE 1.—Materials and their sources of *Sternoptyx* spp.

Species	No. of specimens	Institution[1]	Ship (cruise)	Station	Position	Catalog number
S. pseudodiaphana	1	BMNH	H.M.S. *Challenger*	159	47°25′ S, 130°22′ E	BMNH 87.12.7.151
	1			218	02°33′ S, 144°04′ E	BMNH 87.12.7.157
	6		RRS *Discovery II*	81	32°45′ S, 08°47′ W	BMNH 1930.1.12.43035
	1			85	33°08′ S, 04°30′ E	BMNH 1930.1.12.441
	3			86	33°25′ S, 06°39′ E	BMNH 1930.1.12.552-5
	2			256	34°14′ S, 06°49′ E	BMNH 1930.1.12.411-12
	4			269	15°55′ S, 10°35′ E	BMNH 1930.1.12.413-15
	15		RRS *Discovery* (45)	7824	11°01′ N, 20°11′ W	BMNH 1977.6.14.1-15
	1	IFS	*Walther Herwig*	30/68	36°37′ S, 43°30′ W	
	8			427/71	33°00′ S, 07°50′ E	
	50	IOS	RRS *Discovery* (31)	6662	10°58′ N, 20°00′ W	
	18			7089	17°50′ N, 25°25′ W	
	22			7803	17°50′ N, 25°00′ W	
	48			7824	10°50′ N, 20°00′ W	
	21	LACM	*Eltannin*	1781	39°42′ S, 130°11′ W	
	41			1812	36°38′ S, 87°09′ W	
	27			1835	42°23′ S, 160°14′ E	
	1	MCZ	*Anton Bruun* (3)	160	40°53′ S, 60°01′ E	
	1		(6)	7351	40°51′ S, 64°49′ E	
	1		(13)	5	34°26′ S, 73°28′ W	
	11			6	32°57′ S, 74°57′ W	
	3			10	33°32′ S, 77°56′ W	
	3			15	33°36′ S, 79°32′ W	
	2			20	34°01′ S, 84°58′ W	
	2			41	33°31′ S, 77°29′ W	
	1		*Chain* (35)	962	05°24′ N, 39°55′ W	

APPENDIX TABLE 1.—Continued.

Species	No. of specimens	Institution[1]	Ship (cruise)	Station	Position	Catalog number
	2	USNM	*Eltannin* (21)	3	34°00′ S, 80°36′ W	207241
	19			5	33°06′ S, 83°57′ W	207243
	18			6	33°04′ S, 85°49′ W	207234;207235
	5			8	33°00′ S, 89°38′ W	207236
	7			11	37°12′ S, 94°24′ W	207233
	7			11A	38°35′ S, 95°39′ W	207227
	4			13	39°54′ S, 107°36′ W	207240
	3			15	44°03′ S, 120°17′ W	207239
S. diaphana	2	BMNH	H.M.S. *Challenger*	171	28°33′ S, 177°50′ W	BMNH 87.12.7.152-3
	1			214	04°33′ N, 127°06′ E	BMNH 87.12.7.155
	1	CAS	*Te Vega*	548	35°39′ N, 131°53′ W	
	13	IOS	RRS *Discovery* (21)	6662	10°58′ N, 20°22′ W	
	18		RRS *Discovery* (45)	7803	17°50′ N, 25°00′ W	
	35			7824	10°55′ N, 20°00′ W	
	51		RRS *Discovery* (52)	8281	32° N, 64° W	
	1	LACM	*Valero*	11360	33°20′ N, 118°45′ W	
	1	MCZ	*Anton Bruun* (6)	7247	07°56′ S, 65°14′ E	
	2			7298	22°48′ S, 64°55′ E	
	2			7305	24°22′ S, 64°50′ E	
	1			7352	29°45′ S, 64°58′ E	
	5		(19)	824	19°01′ N, 79°02′ W	
	2			829	19°21′ N, 85°31′ W	
	1		*Chain* (26)	505	12°00′ N, 65°00′ W	
	4		*Delaware* (63-4)	31	NW Atlantic	
	6	MSI	*Bellows* (1)	147	27°00′ N, 86°00′ W	
	3		*Mizar* (3)	166	27°36′ N, 88°40′ W	
S. obscura	1	BMNH	H.M.S. *Challenger*	214	04°33′ N, 127°06′ E	BMNH 87.12.7.156
	1	CAS	*Te Vega*	532	36°40′ N, 122°04′ W	
	1			620	32°48′ N, 118°16′ W	
	1	IOS	*Manihine* (226)		W. Equatorial Indian Ocean	
	3	LACM	*Eltannin*	34	07°47′ S, 81°23′ W	10203
	1		*Valero*		33°20′ N, 118°45′ W	11360
	10	MCZ	*Anton Bruun* (6)	7194	03°27′ N, 65°07′ E	
	10	UANM	*Eltannin* (31)	7A	10°57′ N, 149°19′ W	
	20	SIO	*Monsoon*		11°00′ N, 163°00′ E	
	11		*Tethys*		07°00′ S, 135°00′ W	
	25	ZMUC	*Galathea*		10°24′ S, 114°07′ E	
S. pseudobscura	1	BMNH	H.M.S. *Challenger*	214	04°33′ S, 177°06′ E	BMNH 87.12.7.154
	1			235	37°07′ N, 138°00′ E	BMNH 87.12.7.158
	7	IOS	RRS *Discovery* (21)	6662	10°58′ N, 20°00′ W	
	5		(45)	7803	17°50′ N, 25°00′ W	
	20			7824	10°55′ N, 20°00′ W	
	2		*Manihine* (226)		W. Equatorial Indian Ocean	
S. pseudobscura	1	MCZ	*Anton Bruun* (6)	7237	05°55′ S, 65°10′ E	
	5			7303	24°03′ S, 64°50′ E	
	1		(13)	24	33°48′ S, 90°19′ W	
	13			829	21°25′ N, 85°30′ W	
	1		*Chain* (35)	978	20°00′ S, 28°04′ W	
	3		*Delaware* (63-4)	15	NW Atlantic	
	17	MSI	*Bellows* (1)	142	27°00′ N, 86°00′ W	
	7	SIO	*Horizon*	51375	31°53′ N, 152°21′ W	
	6		*Monsoon*	56133	12°40′ N, 165°09′ W	

[1]BMNH—British Museum of Natural History, London; CAS—California Academy of Sciences, San Francisco; IFS—Institut für Seefischerei, Hamburg; IOS—Institute of Oceanographic Science, Wormley, Surrey; LACM—Los Angeles County Museum, Los Angeles, Calif.; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; MSI—Department of Marine Science, University of South Florida, St. Petersburg, Fla.; USNM—National Museum of National History, Smithsonian Institution, Washington, D.C.; SIO—Scripps Institute of Oceanography, La Jolla, Calif.; ZMUC—Zoologiske Museum Copenhagen, University of Copenhagen, Copenhagen.

BEHAVIOR OF THE HAWAIIAN SPINNER DOLPHIN, *STENELLA LONGIROSTRIS*

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ABSTRACT

The Hawaiian spinner dolphin, *Stenella longirostris*, was recorded from Kure Atoll to the island of Hawaii. It enters atoll lagoons or specific coves or swims over shallow sandy areas, usually near deep water, to rest. Access to nighttime feeding grounds may regulate the location of these rest areas. Rest areas are generally 50 meters or less in depth.

Natural scars and marks allowed study of movements and school structure. Schools are fluid assemblages of variable size and composition. Only small subgroups within schools may have long-term integrity.

Spinner dolphins exhibit several aerial patterns including spinning which is mostly associated with sound production upon reentry, and each is typical of a specific school activity level. Sounds may serve as omnidirectional sound sources maintaining school cohesion beyond the limits of vision.

The daily cycle of spinner dolphins consists of nighttime feeding, morning approach to shore, morning-midday rest, and travel to feeding grounds near dusk. Feeding is upon scattering layer fishes, squid, and shrimp.

Dolphins very commonly show scars from large sharks and from the small squaloid shark, *Isistius brasiliensis*, which scoops disc-shaped pieces of blubber from them. These wounds heal to form dollar-shaped scars.

Most that is known in any depth about the behavior of dolphins has come from observations of captive animals. Yet the environment of captivity, which is at best a pool a few dozen meters in longest dimension and 5 or 10 m deep, can allow only certain aspects of normal behavior to occur. Intragroup relationships may persist, but are usually distorted because relationships seldom remain intact. At best only hints of normal movement and activity patterns can persist where feeding schedules are determined by the workdays of trainers. In nature spinner dolphins, at least, travel constantly, even during rest. Dolphins of many species dive and feed in very deep water.

Thus, however difficult it might be, the naturalist who would study dolphin behavior feels the need to study them in nature. It is usually no simple task. They are wary and travel many kilometers in a day. The presence of the observer almost inevitably causes bias. Dolphins hear exceedingly well, and dolphin schools may be aware of an approaching ship a kilometer or more away.

Our first 2-yr effort (1968-69), with a spotted, or "kiko," dolphin, *Stenella attenuata*, school which we knew to frequent the area within a few kilometers of Kaena Point, Oahu, Hawaii, was abandoned for the reasons mentioned above. It simply proved too expensive in time, money, and effort to work with the animals. Our work was never free from observer bias. Reports of a school of the spinner dolphin, *Stenella longirostris*, (Schlegel 1841), living permanently in Kealakekua Bay, on the Kona or lee coast of the island of Hawaii, caused us to visit the area to see if work was feasible. We found an unusual situation in which several vexing observational problems were ameliorated.

Spinner dolphins do occur in Kealakekua Bay frequently (our figures indicate occupancy about 74% of the time). The bay itself is remarkably good for observation. The Kona coast is normally quite calm, especially in morning hours. Lateral visability is usually 20 m or more. The local people seldom disturb the dolphins. Only cruise boats, which seek out the schools and run through them, are a predictable disturbance. An abrupt 150 m lava cliff backs the bay. Schools sometimes came close to the cliff base at places where our visibility was blocked and could not be seen from the clifftop. But, most of the time we could watch wholly undisturbed schools at reasonably close range, although the distance proved too long for individual identification, and the lack of contrast between animal

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and background defeated good photography. Finally, the bay is relatively small, 3.2 km across its mouth and indented about 2.5 km deep. Its entire area was visible from the clifftop, and usually visibility was good enough that one could see schools well beyond its confines (Figure 1).

These unusual circumstances allowed us to gather new information about spinner dolphin behavior, especially about the diurnal cycle and patterns of movement, though some difficult observational problems remain.

Spinner dolphins proved exceptionally interesting, observational subjects. Not only do they "spin" or leap from the water and revolve rapidly around their longitudinal axis, but they also perform other aerial behavior that can be observed from a considerable distance. These bits of aerial behavior and the sequence in which they occurred proved to be a key to what one might call the emotional or activity level of the school. This level in turn is closely correlated with a number of features of dolphin life, especially the regular sequence of activities during a daily cycle. Aerial behavior, once understood, becomes a predicator of daily activity patterns.

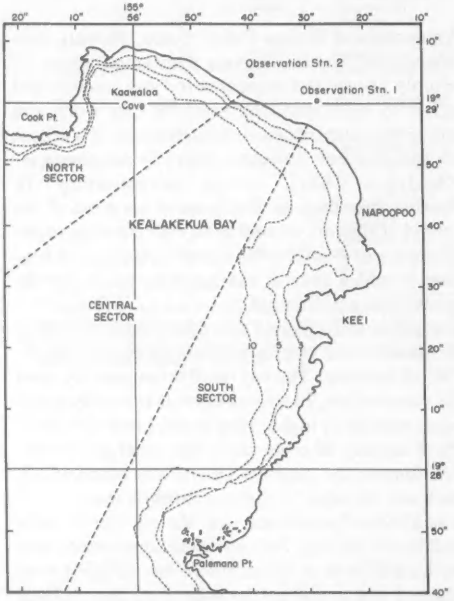

FIGURE 1.—Kealakekua Bay, Hawaii. Shown are observation posts on cliff that backs the bay, shallow-water areas (in meters), and approximate areas frequented by resting schools of spinner dolphins. Also indicated are arbitrary bay sectors used in analysis of arrival and departure directions.

This work, performed in 1970-73, represents a beginning analysis of natural spinner dolphin behavior, a field still in its infancy. Previous reports of the behavior of wild dolphin schools have been mostly single or very fragmentary observations (see Norris and Dohl in press for a review). A few detailed studies exist and allow comparison with this work, such as the work performed by Saayman and Tayler (1971); Saayman, Bower, and Tayler (1972); Tayler and Saayman (1972); and Saayman, Tayler, and Bower (1973), and more recently by Würsig and Würsig (1977); Shane (1977); Würsig (1978); Wells et al. (in press). Saayman and Tayler have analyzed the daily movements of the bottlenose dolphin, *Tursiops aduncus*, and the Indopacific humpback dolphin, *Sousa teuszii*, and their feeding formations and strategies for fish crowding and capture. Würsigs' studies concentrated on Argentinian populations of *Lagenorhynchus obscurus* and *T. truncatus*, while Wells et al. work dealt with *T. truncatus* in Florida.

There are parallels in these works with the behavior patterns described here. The recent work by the Würsigs on the group size, composition, and stability of bottlenose dolphin schools bears similarity. Like ours, much of this work was performed from clifftop observation posts using natural scars and marks to identify individuals. Shane's study, also on bottlenose dolphins, utilized natural scars and marks. Wells et al. carried out extensive tagging studies on Florida bottlenose dolphins. All of these studies and that reported here show remarkable fluidity in school composition and size over short periods of time. The dolphin populations that have been studied, it seems, are not composed of discrete schools of modest size but instead of highly fluid groups that may range considerable distances and may be found associated in very variable combinations of individual animals.

Morphology

Hawaiian spinner dolphins are moderate-sized, slim-bodied, and long-beaked odontocete cetaceans. Adults reach at least 2 m TL (total length), and about 55-62 kg (Perrin 1975). They are handsomely marked animals with a dark gray cape over the dorsal surface, a light gray lateral field (using the terminology of Perrin 1972) sharply demarcated from the cape above, and the white

belly below. The white of the belly extends up the flanks to about the level of the eye. The beak, or rostrum, is dark gray, tipped prominently with black; the lip margins are dark; and the ventral surface of the beak is white. The pectoral fins are dark gray, and a dark flipper band connects its anterior insertion to the eye, which is surrounded by a black eyepatch. Flukes and dorsal fin are dark gray. These color pattern components have been described in more detail by Perrin (1972), and they have been compared with the patterns of geographical forms of spinner dolphins living in the eastern tropical Pacific. In nature, against the blue or turquoise backdrop of tropical water, the dark pattern components of spinner dolphins appear in shades of brown, but the effect is usually lost when the animals are removed from the water. The white and other pattern marks are often suffused with pink, from superficial blood flow in the blubber, which may also contribute to the overall brownish cast of pattern components in living spinners.

Systematics

In recent years a worldwide picture of the distribution and systematics of tropical odontocetes has begun to emerge. Well-documented collections, often with measurements and photographs, have been made from all oceans, especially where dolphins are involved in fishery operations (Kasuya et al. 1974; Perrin 1975). A special beneficiary of this work has been the once chaotic genus *Stenella*. It now seems reasonably clear that the genus is composed largely of three major species or species complexes: the spinner dolphins, allied to *S. longirostris* of the Hawaiian Islands; the striped dolphin, *S. coeruleoalba;* and the spotted dolphins, allied to *S. attenuata* of the Hawaiian Islands. All are tropical or subtropical. All are often found far offshore or near islands.

In the eastern and central Pacific, Perrin (1975) discerned four geographical forms of spinner dolphins: 1) a Costa Rican long-snouted form occurring close to the Central American coast, 2) an eastern form occupying the open sea from the American coast out to long. 115° W, 3) a whitebelly form occupying the open ocean both south and west of the eastern form (and overlapping with it to some extent) to about long. 145° W and nearly to lat. 5° S, and 4) an Hawaiian form localized around the Hawaiian island chain. Perrin (1975) stated that Hawaiian spinner dolphins are most closely related to the adjacent whitebelly form, differing from them by being somewhat more robust, by having a larger area of white belly coloration, and by lacking the speckled margins of the white belly field. He places the complex tentatively in the species *S. longirostris*.

Most of the races of spinner dolphins from around the world are quite similar to the Hawaiian form. Only the Costa Rican and eastern forms are strikingly different, being nearly uniform gray, with faint hints of pattern components found in other races. These aberrant forms also show remarkable sexual dimorphism, which is otherwise rather subtle throughout the species. Fully adult males of these two races often possess a dorsal fin that is canted sharply forward, "like it was stuck on backward," and a very heavy postanal protuberance. The fin of Hawaiian spinner dolphins is either triangular or very slightly falcate, and only a subtle postanal protuberance can be noted in adult males.

METHODS

A camp was established on the Greenwell Ranch at the edge of the cliff overlooking Kealakekua Bay (Figure 1). Two observation sites were used for recording and observation by telescopic means. Observer teams kept regular watches during daylight hours.

Several vessels were used for observations at sea, or to provide an anchored platform in the bay, including the brigantine *Westward* and the motor sailers RV *Hikino* and the RV *Imua*. A trip through the northwest Hawaiian chain was made on the U.S. Coast Guard buoy tender *Buttonwood*.

Fourteen spotting flights were made throughout the main Hawaiian chain, mostly from small fixed wing aircraft.

Underwater observations were made in a specially built underwater observation vehicle or mobile observation chamber (MOC) 6 m long, which looked like a small submarine (Figure 2) but did not submerge. It consisted of a float made from an auxiliary aircraft gasoline tank and a central observation chamber. The viewer in this chamber below water obtained ventilation from a squirrel cage blower and was surrounded by a band of Plexiglas[2] windows at eye height. Controls for turning or tilting the craft were at hand, and a

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

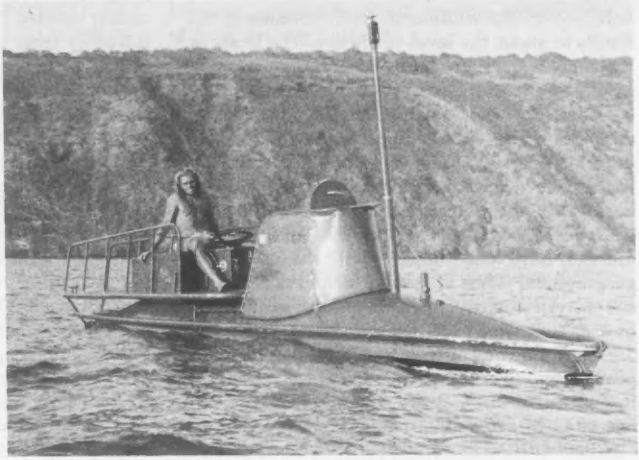

FIGURE 2.—Mobile observation chamber (MOC) at Kealakekua Bay. The hatch is open to a cylindrical observation chamber that projects 1.5 m below the hull. The observer views through a 360° band of Plexiglas windows. The operator steers and operates the engine.

tape recorder was connected to a hydrophone[3] mounted amidships and oriented forward.

The craft was run by an outboard engine set in a well aft. Stability was maintained by 900 kg of lead blocks in a compartment below the observers feet.

Other underwater observations were made with scuba, or by putting an observer with snorkle or scuba below the bow of a slowly moving skiff, holding onto a bow painter. In this way the observers could sometimes be towed among the animals and even be jostled by them. A field station was established at the village of Napoopoo on Kealakekua Bay.

Feeding was observed from skiffs and larger vessels. Dip net samples were taken in the region of feeding, and stomach analysis of such specimens as became available to us were collected. The squid and crustaceans in stomach samples were identified by Richard Young of the Department of Oceanography, University of Hawaii. Fish otolith collections were lost through improper preservation.

Recordings were made with a hydrophone deployed from a stationary skiff located near a school of animals or from the MOC. Monitoring was by use of headphones. During our studies we were fortunate to have William Schevill and William Watkins of the Woods Hole Oceanographic Institution establish a four-hydrophone array deep in Kealakekua Bay. With this apparatus, three-dimensional tracks of passing dolphins were obtained that were of greater range and fidelity than allowed by our simple gear. The experimental arrangement of this array and recording characteristics are described in Watkins and Schevill (1974).

Dolphin radiotracking used dolphin dorsal fin radios (see Evans 1974) and a hand-held direction finder. Dolphins were captured by a standard head net.

Throughout this paper we use the term "school" to indicate all animals in a discrete area that move together. Such schools are often composed of recognizable, discrete "groups" of animals clustered together and moving and diving more or less in unison. For instance, while the direction of movement of larger schools may be the same for all its parts, diving synchrony for all animals may be quite extended and ragged, being composed of a number of synchronously diving groups. Within such groups one can sometimes recognize small "subgroups" of a few (2 to perhaps 12) animals that are often seen together, regardless of the group or school composition around them.

DISTRIBUTION

Marine mammal collectors of the Sea Life Park, an Hawaiian oceanarium, suggested that spinner dolphins occur habitually at certain areas along the island shores, while they are largely or wholly

[3]An Atlantic Research Corporation LC 32 hydrophone, a Hewlett-Packard 456A preamplifier, and a Uher 4000s ¼-in tape recorder composed the recording gear. The upper frequency response of this system was approximately 20 kHz at 7½ ips.

absent from others. This led us to collect sighting and capture locations for the entire Hawaiian chain. The same collectors reported that after collection of animals from a given school, the school as a whole might become shy of the boat for an indefinite period, and suggested that it occupied a given area of coast and the school might have integrity through time.

We found that spinner dolphins occur throughout the Hawaiian chain, from its northwesternmost limit at Kure Atoll (lat. 25°40′ N, long. 175°38′ W) to its southernmost limit at South Point, or Ka Lae, on the island of Hawaii (lat. 18°49′ N, long. 155°41′ W). Occurrence is not random, but spinner dolphins are gathered in small to moderate schools (6 to about 250 animals) near all major islands and shoal areas and can be found with some regularity near certain shoals or coves. Only near small islands that drop abruptly without having significant shoals, such as at Nihoa Island, have we not found spinner dolphins. The following is a synopsis of known spinner distribution. Unless otherwise specified, all sightings were by the authors. Specific records are shown in Figure 3.

Kure Atoll. On 3 September, 1971, Norris visited Kure Atoll. The commanding officer, Lt. (j.g.) Joel Greenberg, reported having seen a school of 20-30 spinner dolphins enter a west pass into the atoll lagoon. Without prompting he described their spinning behavior.

Midway Island. On the midafternoon of 3 September 1971, a school of approximately 35 spinner dolphins was noted in shallow water at the edge of the channel inside of Eastern Island. The regular daytime occurrence of animals in the shallow atoll lagoon was reported to us by residents of Midway.

French Frigate Shoals. On 12 September 1971, at 0830 h, 30 animals were noted just off Shark Island, spinning and leaping.

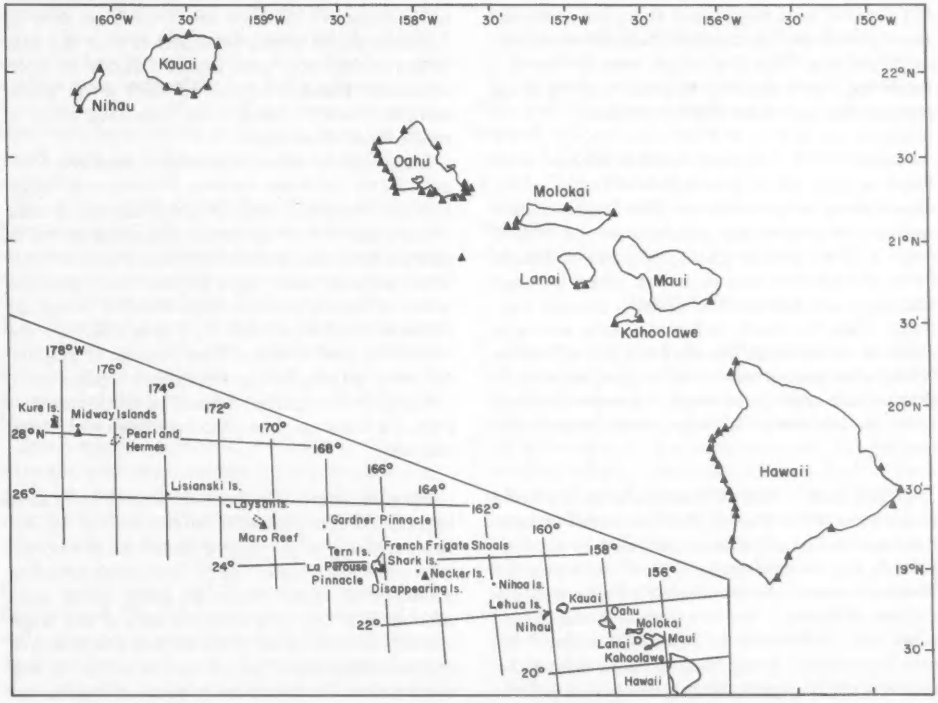

FIGURE 3.—Sightings of spinner dolphin schools by the authors (triangles) in the Hawaiian Island chain.

Pearl and Hermes Reef. Edward Shallenberger reported seeing a spinner dolphin school at this location in the fall of 1978, entering the central lagoon during the day.

Necker Island. On 13 September 1971, 10.2 mi east-southeast of Necker Island at 1600 h, a school of about 30 spinner dolphins was seen.

The following localities in the northwest Hawaiian chain were visited without seeing spinner dolphins; Salmon Bank, Lisianski Island, Laysan Island, Gardner Pinnacles, and Nihoa Island. Five to 10 animals that may have been spinner dolphins were seen 18.5 mi, 134° T from the wreck at Maro Reef, by Ens. Albert Sarra, U.S. Coast Guard, on 9 September 1971.

Niihau Island. Spinner dolphins have been sighted at Kaumuhonu Bay (60 + animals) at the southwest tip of the island, between Lehua Island and Kikepa Point (20 + animals); smaller schools (15 + each) have been noted along the southeast shore near Pueo Point and on the northwest shore at Nonopapa. The Nonopapa record was of a traveling school that moved close to shore along perhaps half of the northwestern coast.

Kauai Island. Spinner dolphin schools were found around Kauai Island at 3-16 km intervals, except along its western coast. The largest schools were estimated at 150 animals on the Napali coast, a 70-80 animal school just north of Kahala Point, and an estimated 60 animal school between Hanapepe and Kaumakani. Smaller schools, scattered along the south and east coasts, averaged about 15-30 animals. The only obvious difference between the vacant coast and the occupied areas is that vacant areas have much narrower, shallow water shelves devoid of deep indentations in the coastline.

Oahu Island. Records from the various sources over 14 yr (1962-76) show that two broad areas of the coast are nearly always occupied by spinner dolphin schools during the day. First, along the Waianae coast between Barber's Point and the vicinity of Kaena Point (the west or Kona shore), schools estimated between 30 and 100 animals can nearly always be found close to shore during the day. Second, an apparently larger school or schools is often seen in the coastal area between about Pearl Harbor and Makapuu Point. Schools of animals seen in this area have been estimated to number from 40 to 250 individuals. Small schools have been seen near Kahana Bay and Waimea Bay. Because this is the windward coast, subject to almost constant tradewinds, little collecting effort has been expended there and dolphins may be more common than our records indicate. A relatively narrow shelf (1.6 km) exists along the Waianae coast except at Kaena and Barber's Points where it broadens considerably. The shelf around the remainder of the island is much broader, averaging about 4 km, and is marked on the northwest and northeastern coasts by a fringing reef.

Molokai-Lanai-Kahoolawe-Maui. Geologically this four-island complex has resulted from one series of volcanic eruptions, producing islands with interconnnecting shallow areas and channels. Spinner schools have been seen at several locations around the margins of this complex, but seem rather seldom to travel to inshore locations over extensive shallow areas such as that at Lahaina Roads (Auau Channel) or over the flats between Molokai and Lanai Islands (Kalohi Channel). Dolphin schools in such areas would have to travel 11 km or more from deep water to reach these shorelines.

Large spinner schools have been seen over Penguin Bank (between western Molokai and Lanai Islands), the south coast of Lanai, especially near Manele Bay (40-100 animals), and along the south shore of Kahoolawe, especially near Halona Point; small schools were seen on the north Molokai shore at Kalaupapa and Cape Halawa, along the Hana coast of Maui, and at Lipoa Point on the northwest end of Maui. Two records of spinner dolphins accompanying humpback whales near Lahaina were reported to us. The bottlenose dolphin, *Tursiops* sp., has often been seen with these whales.

Hawaii Island. Spinner dolphin schools have been found at scattered locations around the entire periphery of the island except for the northeast shore, though there are some shorter stretches of coast where we have never seen schools. It is not surprising, in view of the large size of this island, that there are more localities of regular occupancy by porpoise schools than for any other island. We found seven areas of regular occupancy and four localities with more transient occupancy.

On the lee side of Hawaii, the largest school was centered at Keahole Point, ranging along about 23 km of coast, from Honokohau Harbor to Kiholo Bay. In all, there are estimated to be about 200-250 animals generally occurring in this area, and they may be found in a single school at times or fragmented into two or three smaller schools, separated by a few kilometers of coastline. Here, the dolphins do not seem to occupy any of the small coves consistently, but to congregate over the rather extensive area of shallow water, moving back and forth. Not uncommonly, parts of this aggregation moved during the day beyond the limits listed above and may move as far as Kailua-Kona or beyond, though the constant sea traffic in that harbor seems to prevent normal daily quiescence (defined below). We have termed these animals collectively the "North Kona School." Twenty-eight kilometers to the south, at Kealakekua Bay, a school ranging from 2 to 70 animals (average 25 animals over 73 observations) was found. In our observations, dolphins occurred in this bay on 74% of 113 observation days. They most commonly occupied the deeply indented bay but sometimes were found on the shallow area north of the bay to Keauhou or occasionally nearly to Kailua-Kona. Less commonly they were found to the south in or near the very small bays at Honaunau (City of Refuge) or Hookena.

The entire 56 km stretch from Hookena to South Point seems not to harbor spinner dolphin schools on a regular basis, though it should be noted that a military air closure zone prevented our flying over the Milolii area regularly. We have a single record of a 20 animal school at Milolii. This precipitous coast drops abruptly into deep water, without shallow areas alongshore. Much of the coast is composed of relatively new lava flows from nearby Mauna Loa volcano.

Small schools, estimated generally at about 20 animals, were seen, usually in very rough water, at South Point, between Ka Lae and Honuapo, over the modestly developed shallow area there, or occasionally in the deep cove at Kaalualu.

At Keauhou Cove, directly below Kilauea Crater, a small school (20-25 animals) was consistently found. The dolphins came into very shallow water there in an area protected by Keaoi Islet and flanking coral heads, which produce a small area of calm water along an otherwise rough water coast.

Cape Kumukahi, the easternmost point on the island, hosted a population of about 30 animals. Several small irregular bays along the southern edge of the cape form the "home bay" in this area, with animals being noted at times as far as Opilukao Cove.

The largest school on the windward shore (ca. 100 animals) was often found at Kaloli Point, 18 km south of Hilo Bay. This location seemed also to be the northernmost area of occupancy on this side of the island. The dolphins were typically found in the bay protected by the point and fringing coral reefs. The rather shallow bay (maximum depth 20 m) is close to deep water to the south.

The 112 km stretch of coast from Kaloli Point to the north end of the island (Upolu Point) seemed devoid of resident spinner dolphin schools. It is also the site of the major sugar cane processing plants on the island. Effluent from these plants seems to produce murky waters along the coast and clearly contributes to the long drift lines of flotsam from processed sugar cane. Whether the absence of animals and this activity are related is unknown.

At the north tip of Hawaii we occasionally saw or heard of small schools of spinner dolphins (10-30 animals) in the area between Kawaihae Bay and Honoipu, though more often the entire stretch of coast was found to be without animals from the Kiholo Bay to the north tip at Upolu Point. This circumstance is anomalous, in that well-developed, shallow-water areas occur along this shore, where schools might come during the day, and where the sea is generally calm.

REST AREAS

Three features of the distribution of spinner dolphins in the Hawaiian chain stand out. First, the distribution is discontinous. Some coasts may have several areas where dolphins congregate, and others may have stretches of many kilometers in extent where no amimals are seen. Second, certain coves or shallow areas are clearly regular aggregation sites, while others seem to be used much more infrequently. Third, some areas consistently carry more animals than others. As we will demonstrate, spinner dolphins come inshore during daylight hours to enter a quiescent period of some hours duration, and we think of these congregation sites alongshore as "rest areas."

What typifies such rest areas? First, all rest areas are shallow sandy areas with <50 m depth over part of their extent. They are usually com-

posed of a mixture of open sandy bottom dotted with coral formations. Coves may or may not be present. All rest areas are close to deep water. Usually water >500 m depth can be reached within a few kilometers. Some schools, such as those in the Waikiki (Oahu) or Manele Bay (Lanai) areas, have access to considerably shallower water than others. Schools living there may be restricted to waters no deeper than about 600 m since our observations on the Kona coast of Hawaii indicate that schools do not move more than a few kilometers from shore at night. Other schools, such as at Keahole Point (Hawaii) regularly move into water >2,000 m depth. Of course, the observations we have made on the island of Hawaii may not hold elsewhere.

Apparently spinner dolphins only occasionally travel onto extensive shallow areas like that at Lahaina Roads (Auau Channel), which is about 24 km long. Instead they typically congregate along its margins, along the south shore of Lanai Island and Kahoolawe Island, where deep water is nearby. The areas most closely studied here are Kealakakua Bay and Keahole Point, both have deep water accessible within 1.5-2.5 km of shore. The inference is that rest areas are chosen by dolphins not only for physical characteristics such as depth, bottom type, and perhaps calm water but also for their accessibility to nighttime feeding areas.

Spinner dolphin schools also rest in atoll lagoons. At Kwajalein Atoll, on 10 September 1973, at 1630, a school of about 40 spinner dolphins was noted about 1 km inside Bigej Pass. The school was moving toward the pass, presumably on its way out to sea. A local resident told us that the school was regularly in this pass and not found in other nearby passes into the central lagoon. Similar observations have been made at Kure Atoll, Midway Atoll, and near Shark Island at French Frigate Shoals. The animals (approximately 35), resting quietly in a shallow channel not far inside Eastern Island at Midway, were sighted from a helicopter. Probably wherever atolls and spinner dolphins occur together the animals use the atoll lagoons for rest.

In the eastern tropical Pacific a large spinner dolphin population occupies oceanic areas far from land. In view of the use of shore situations elsewhere in the range of the species, one wonders what, if any, substitution is made. Norris and Dohl (in press) have speculated that the frequently observed association between spinner and spotted dolphins in the eastern tropical Pacific (this association does not occur in Hawaii) may hold the answer. Spinner dolphins may seek the schools of spotted dolphins for refuge during rest in the open sea. We believe this may be true because spotted dolphins feed during the day, while spinners are nocturnal feeders, and spinner dolphin schools have been observed to join spotted dolphin schools in the morning (Norris et al.[4]). If such rest association occurs, the spinner dolphins are associating with alert animals in this oceanic area. Related to this the yellowfin tuna seine fishermen chase and encircle dolphins to catch tuna, most fish apparently follow the spotted dolphins. Since the association between tuna and dolphin is probably food based, the tuna may be following the dolphin species that is actively searching for food. That is, like the tuna, the spinner dolphin may follow active dolphin schools.

Spinner dolphins resting along shores maintain a continuous but slow locomotion, and it seems likely that the searching or feeding activities of spotted dolphins would not greatly change these requirements for rest.

MARKED ANIMAL STUDIES

Dolphin schools are seen frequently at the same localities while other areas never seem to harbor them. Are these schools of resident animals, or are they composed of transients that for some reason choose certain regions of the coast for rest? The frequent observation of dolphin collectors that a given school will avoid their vessel after animals have been collected from it (Norris and Prescott 1961) indicates possible residency. On the other hand, dolphin schools are not always in these rest localities, and the number of animals using a given cove may vary widely from day to day. This indicates fluidity in school structure and variability of school movement. Such fluidity has been noted for other porpoise schools by Würsig and Würsig (1977) and Saayman and Tayler (1979).

Because we were concerned that the spinner dolphins of the Kona coast of Hawaii should not fear our vessel, we sought to recognize individuals by natural scars and marks rather than by placement of tags. Ultimately we were able to catalog 50 recognizable individuals and resight-

[4]Norris, K. S., W. E. Stuntz, and W. Rogers. 1978. The behavior of porpoises and tuna in the eastern tropical Pacific yellowfin tuna industry-preliminary studies. Natl. Tech. Inf. Serv., Final Rep. No. MMC76/12 PB 283-970, xi + 86 p.

ings provided a partial picture of the school and individual movements. Our shipboard work with dolphin schools was restricted almost wholly to Kealakekua Bay through most of 1970. Only toward the end of that year and during 1971 and to a limited extent later, much sea time was spent in other areas. Hence a large proportion of our sightings do not bear on the question of dispersal distances or rates by individual dolphins. We gathered no information on possible interisland movements.

By far the most useful scars and marks were those of the dorsal fin. Twelve of our animals were in this category (Figure 4). These animals could be resighted from shipboard, and sometimes from considerable distances. It is not surprising that 49, (64%) of our 76 resightings were of these animals.

Many marked animals had scars or pattern peculiarities. Such marks could only be sighted on dolphins at the bow of the observation vessel, or from our MOC. The MOC was used sparingly because it was noisy and disturbed dolphin schools and because it was safe only in calm seas. Thus, information on repeated social associations within schools is limited to two sets of sightings and journal notes over 14 days, all within Kealakekua Bay. In any school only a few individuals swam at the bow of a vessel, while others stayed well clear, thus reducing the chances of sighting many animals. Of 38 animals cataloged with body scars or marks, there were 27 resightings. The final marked animal recorded was an individual with a vertical white stripe on its dorsal fin (Figure 4).

Our store of recognizable animals built up slowly over the entire period of the study, thus making interpretation of movements difficult; nonetheless, some important ideas emerge: 1) No resident school permanently and regularly uses a given cove or local region of shoreline. Instead, each cove or resting spot may harbor a given subgroup of dolphins for a matter of days or weeks. 2) Schools are labile mixtures of groups and subgroups. 3) Individual movements may span the entire Kona coast, or even beyond (true ranges of movement remain unknown). A few "marked" individuals have been seen over rather long periods, but other equally recognizable animals have been seen only briefly, or never again

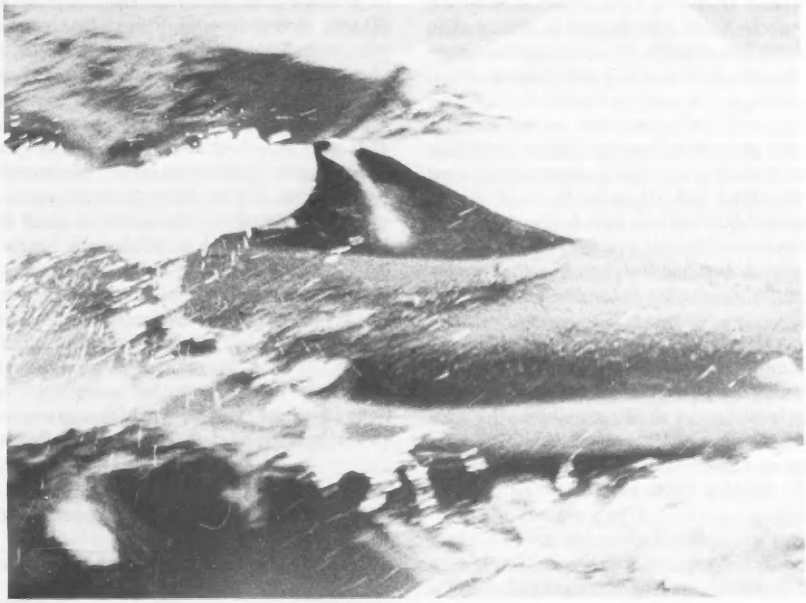

FIGURE 4.—Spinner dolphin with vertical white stripe on both sides of its dorsal fin. We suspect that this animal had shed a radio pack after the pin had migrated out of the fin.

after an initial sighting, suggesting either rapid population turnover or high levels of intermixing between the various schools of the area.

Two pale animals were seen. They were very different visually from their associates. This was especially evident from the air. They were seen along the entire southern Kona coast from Keahole Point to Kamilo Point east of Ka Lae (South Point) and over the longest time span for any "marked" animals (1,220 days out of the total 1,246-day recording period). These pale animals were seen either alone or on occasion together in the same school. These data are suggestive only, because such pale coloration cannot be assigned definitely to a given animal since it is a recurrent condition in the species. For example, such a pale animal was captured near Oahu, and for some years was an exhibit animal at the oceanarium, Sea Life Park. The animal, called "haole" for "white person", gradually grew darker during captivity but always remained slightly pale. Perrin (1972) described a pale animal from the eastern tropical Pacific, as "albinistic."

Let us examine each of our conclusions in turn. First, is the question of residency. Taking only those animals recognizable from the surface, we find that 7 of 12 animals were seen in both the large Keahole Point schools and in the smaller Kealakekua Bay schools. The pale animals were seen both in Kealakekua Bay and Keahole Point schools and far to the south at Kamilo Point. There were long periods when a given animal was not seen at one or another locality. This information cannot be usefully quantified because schools were sometimes large and all animals could not be examined and because our records are not the result of concerted attempts to check each animal in a given school. Instead, the records reflect opportunistic sightings during the pursuit of other activities.

Animals clearly moved back and forth between the Keahole Point and Kealakekua Bay assemblages. Of the 12 animals, 6 were seen at more than one locality and then returned to the first locality of sighting at least once. Three animals were seen at a single locality only, but this may reflect low sighting frequency rather than lack of movement.

Finally, three animals were seen at two or more localities but did not return to the locality of first sighting. For these reasons we reject the idea of a given cove having a definable resident school (Table 1).

TABLE 1.—Movement of Hawaiian spinner dolphins that were identified by natural scars and marks.

Dolphin number	Total time observed (days)	Maximum distance travelled (km)	Number of sightings
1	293	18	3
23	183	0	3
24	1,096	36	14
30	342	36	11
32	246	0	3
39	236	36	3
40	275	36	4
44	170	36	6
45	1,220	113	7
46	862	10	3
49	39	36	2
50	1	0	1

Reversals = 6
One location = 3
Two or more sequential locations = 3

Our data are too incomplete to show how long a given animal might spend at a single locality, or how often it switches between rest localities. Only the number of consecutive days during which a given surface-visible marked animal was seen at a single locality vs. the number of days of consecutive observation during the sighting period is indicative. Considering the animals for which most resightings are available: numbers 24 and 30, during four separate continous periods of observation of 9, 8, 9, and 10 days, animal 24 was seen 2, 2, and 3 days consecutively (Table 2). Animal 30 was seen only once, 2 days in a row, during consecutive observation periods of 7, 10, and 10 observation days. Animal number 13 (a large calf traveling with its mother) was seen three consecutive days during a 16-day observation period at Kealakekua Bay. During consecutive observation periods in which the observer moved from Kealakekua Bay to Keahole Point, certain animals were noted on consecutive days at the two localities, indicating a switch in a single night from one to the other. These data indicate that movements are frequent, at least between the Kealakekua Bay and Keahole Point rest areas.

As for the conclusion that dolphin schools consist of labile aggregations of groups and subgroups, the best information comes from fluctuations in school sizes with which a given marked animal was associated. The results reflect almost

TABLE 2.—Occurrence of a single spinner dolphin (No. 24) and the size of schools in which it was seen at Kealakekua Bay, Hawaii, 1970.

Dates of observation	Estimated school sizes	Number of times seen
28 Apr.-6 May	15-30	3 days of 9
23 June-30 June	15-40	2 days of 8
10 Sept.-18 Sept.	25-36	3 days of 9
28 Oct.-6 Nov.	7-120	3 days of 10

the entire range of school sizes observed. For example, at various times number 24 was found in schools varying from 7-10 to 120 animals, and number 30 covered about the same school size range, from 6 to 150 animals. Observations from the MOC showed that on one occasion the same subgroup, with the same general internal arrangement of animals, persisted for at least 3 days. Many times, during three consecutive observation days (25-27 March 1970) the same subgroup of five animals came to the bow of the MOC. This sort of asssociation is well known in captive schools and persists for long periods of time (McBride and Hebb 1948; Tavolga and Essapian 1957; and Bateson[5]). Such groups in captivity may be constructed of related or nonrelated animals or even of animals of different species (Bateson see footnote 5). Thus, while our observations of wild schools do not provide proof, we expect that some subgroup structure may persist over long periods and that familial lineages may be important, as has been observed in captivity (Tavolga and Essapian 1957).

The role of subgroups in larger dolphin schools is apparently not simple. Such schools are not simply composed of groups and subgroups that themselves have cohesion. Instead, there are also some assemblages that seem typical only of large schools. For example, in large schools, groups are often segregated. Groups of juvenile animals or of mother-young pairs may be seen. Large schools differ from one another by the presence or absence of such groups. Some schools were composed only of adults, while others had a high proportion of young animals. Subgroups may move between schools. Some social ordering, largely related to growth and reproduction, may take place in schools regardless of the origins of their constituent parts. A major force in such ordering within large schools may be the aggression of certain large adults, that may be either male or female, who herd vulnerable groups to central locations within the school (McBride and Hebb 1948). Such patterns have been proposed for *S. coeruleoalba* by Kasuya (1972) and for *S. attenuata* by Kasuya et al. (1974).

AERIAL BEHAVIOR PATTERNS

An experienced observer of spinner dolphins can quickly judge the activity state of a school by watching its aerial patterns. It is possible to judge the alertness of school members by checking the kind and frequency of aerial patterns. In fact, such analysis soon makes it obvious that the entire sequence of changing behavior patterns through any 24-h cycle is related to the level of activity, or "emotional state," as indicated by aerial patterns.

Spinner dolphins not only "spin" but perform several other clearly recognizable aerial patterns. These include leaps, tail-over-head leaps, backslaps, headslaps, noseouts, and tailslaps, or a combination of these patterns—each performed with variable vigor and frequency at various times of day.

The spin. The spinner dolphin rushes to the surface as if about to make an arcing leap, and at the last instant, when most of its body is out of water, tips its flukes slightly and flexes its tail stock, causing the airborn animal to spin about its longitudinal axis. As many as four revolutions may be made in the course of such a leap (Hester et al. 1963). The dolphin may literally appear to flicker as flippers, flukes, and the dorsal fin flash by. The animal falls back into the water, usually partly on its side, and its rapidly rotating body scoops out a hollow of water around the sinking animal. The hollow then collapses producing a welter of spray (Figure 5) and a discernible clap of sound. The spin is enhanced in air by postural movements, in addition to the momentum initially imparted when leaving the water. Just as a gymnast flexes his or her body or as a skater moves elbows in a spin, the spinning dolphin flexes its head and tail and moves its flippers toward or away from its body (Figure 6).

Spins are usually performed in a series of descending intensity (as are other aerial patterns). A given animal may spin as many as a dozen times in succession, each successive spin generally being of somewhat reduced intensity compared with the last. The first leap may reach an apex perhaps 3 m above the surface, while in the last of a series the animal may not clear the water at all. Most spin series are short, being composed of three or four spins.

All age-classes spin. It is not uncommon to see small calves spinning repeatedly in moving schools. In one case a young animal leaped into a spin while in a feeding school, landing a dozen meters off our bow. Each successive spin brought the animal closer to us, as it was seemingly oblivi-

[5]Bateson, G. 1965. The cetacean community in Whaler's Cove-Sea Life Park.

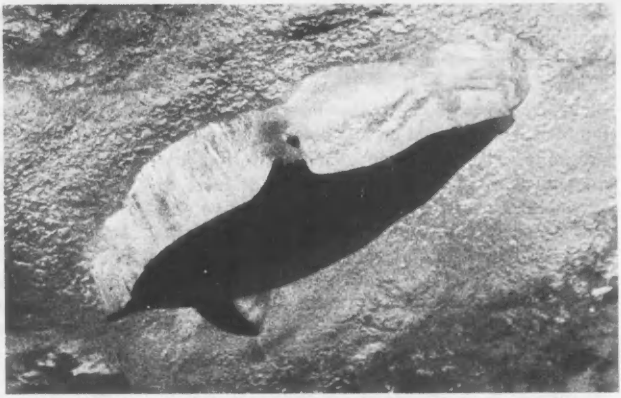

FIGURE 5.—Spinner dolphin reentering the water after a spin, seen from below. Note the longitudinal hollow of water scooped out by the rotating animal. Photo by Henry Groskinsky, courtesy Time, Inc.

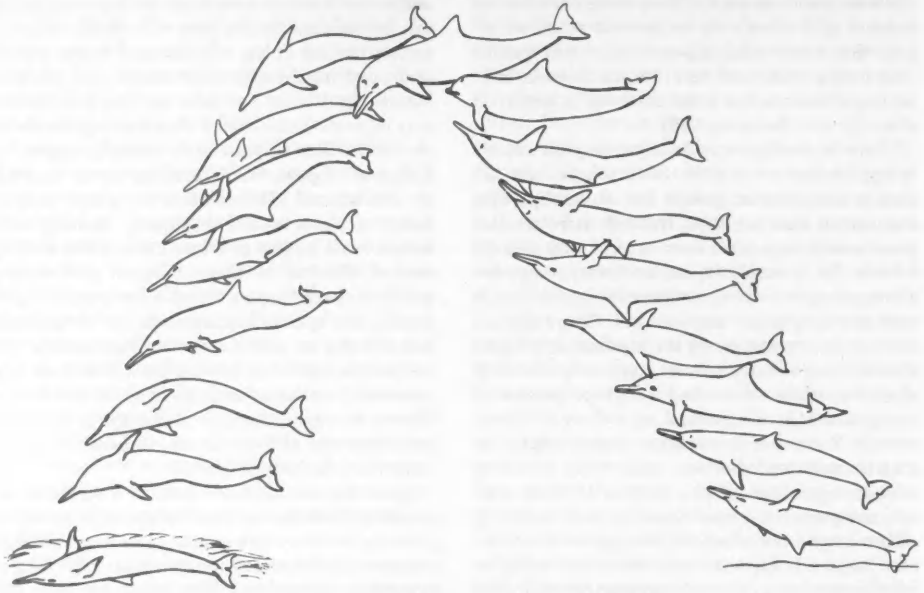

FIGURE 6.—Body postures of spinner dolphins during a spin. Vertical and horizontal dimensions of leap not to scale. Redrawn from Hester et al. (1963).

ous of our presence. The last spin launched the animal nearly at the bow; it fell back into the ship's bow wave, startled, and swam rapidly away below the surface.

Spins may be seen in all parts of a school. Leadership or dominance do not seem to be the obvious factors in spinning behavior. In fact, the opposite could be true since very young animals spin, and in our observations of captive spinner dolphins a high frequency of spinning was observed in an animal that had not been socially accepted into the resident captive school. The best correlation of frequency of spinning and the condition of a school seem to relate to alertness, or activity level of the animals involved, the greater the alertness the more frequent the spins. The more spread out a

school the more frequent spins seem to be. In feeding schools, which are the most dispersed of all school formations, spinning and other high energy aerial behavior occur almost continously.

The leap. The most common aerial behavior in which spinner dolphins actually leave the water is the leap. Spinner dolphins perform leaps by bursting from the water at about a 30° angle, rising a meter or two above the surface, and falling back into the water on the belly or side in a welter of foam. Less frequently, reentry may be made cleanly, snout first.

Tail-over-head leap. The most active and perhaps physically demanding aerial behavior pattern is the tail-over-head leap and its variant, the tail-over-head leap with spin. These aerial patterns are seen only when the Spinner dolphin school is most active. In this pattern the animal bursts from the water at a rather high angle, slings its tail over its head in a wide arc, usually trailing a spiral of spray and enters tail first, often slapping its flukes against the water with a loud "thwack" in the process (Figure 7). On occasion this may be accompanied by one or two revolutions of a spin at the same time.

Backslap. The animal leaps about half or a little more of its length out of water at about a 30°-45° angle, upside down. As it falls back, it arches its body sharply, giving the water a sharp slap with the dorsal surface of its head and beak (Figure 8). Backslaps are often performed in slowly moving schools.

FIGURE 8.—A typical backslap of a spinner dolphin. As the school moves slowly the dolphin emerges in the direction of swimming, belly up, and arches its back at the last instant and slaps its back against the water.

Headslap. The reverse of the backslap. The animal emerges in the normal position, once again at about 30°-45° angle to the water surface, and then flexes its head sharply downward, slapping its chin and lower beak against the water (Figure 9). It is one of the most common patterns seen in moving schools.

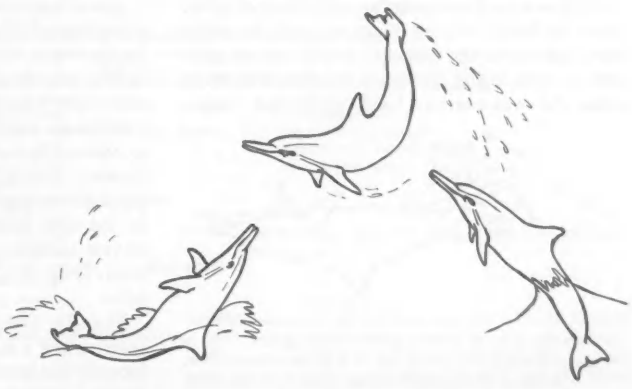

FIGURE 7.—The tail-over-head leap of a spinner dolphin. This may, at times, be combined with a spin.

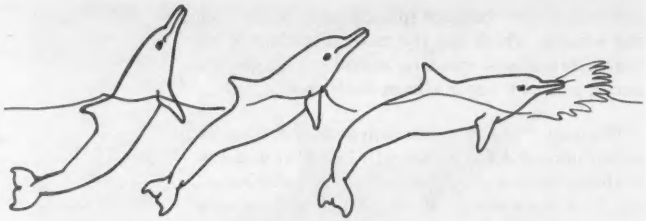

FIGURE 9.—A headslap. The spinner dolphin emerges belly down in the direction of swimming and flexes its body forward sharply at reentry.

Noseout. The least active aerial behavior. The spinner dolphin simply arches its back as it swims to the surface, raising its snout into the air. It is sometimes seen briefly when a resting school is disturbed, or in schools where other, more active behavior is occuring. It is often the first aerial behavior seen in an awakening school.

Tailslap. This pattern may be performed in either the normal or the inverted position. With the dolphin at the surface the tail is arched, bringing the flukes above the surface. The flukes are then brought down smartly against the water producing a clearly audible sound. In the inverted position an animal may sometimes scull along making repeated and rapid tail slaps in a behavior we have called "motorboating," because it not only leaves a continous wake, but makes a "pop pop pop" sound. An animal may slap 10 to 20 or more times in succession in this way (Figure 10). A whaler's term, "lobtailing," describes the same behavior, but seems less descriptive than "tailslap," a term now widely used by porpoise trainers.

What are the functions of aerial behavior? A key point, we feel, is that each pattern, with the possible exception of the noseout, clearly makes noise and, in fact, seems primarily structured to make noise. For example, in a headslap the last component of the pattern is a rapid flexure of the trunk and neck causing the chin and throat to slap against the water. The tail-over-head leap effectively slaps the flukes against the water with great force. The spin scoops a cavity from the sea surface whose walls collapse and thus produce a sound we have heard both above and below the water. Other aerial patterns are similarly structured. Such sounds probably radiate in all directions. Dolphin sound generation and beaming apparatus, on the other hand, transmits sound in a structured beam, directed forward (Schevill and Watkins 1966; Norris and Evans 1967; Evans 1973). This beaming is better known for clicks than whistles or burst pulse signals, though apparently also true of the latter, at least in the killer whale, *Orcinus orca* (Schevill and Watkins 1966). The directionality of clicks has been discussed for *S. longirostris* by Watkins and Schevill (1974). Thus, while vocal signals are directed almost wholly in certain sectors, the sounds of aerial behavior are likely to approach omnidirectionality. Our recordings indicate that none of the signals of aerial behavior propagate long distances. Tail slaps may be the loudest.

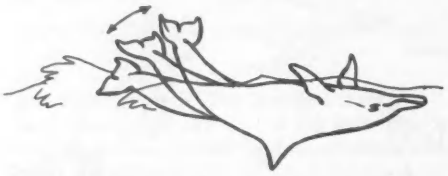

FIGURE 10.—An inverted tailslap by a spinner dolphin. Tailslaps also may be made in normal body posture. Often a series of a dozen or more slaps may be made at a single time, which has been termed "motorboating" because of the white wake and the sound produced.

Aerial behavior is most frequent in fully active schools in which the animals are dispersed, sometimes rather widely. In tight resting schools (see below) sounds of all kinds except for desultory clicking are nearly absent. Conversely, our observations of a captive spinner dolphin school held in a community tank at the Oceanic Institute, Oahu, Hawaii, showed that aerial behavior continued through the night and, in fact, was most frequent in the dark. Thus, high frequencies of aerial behavior seem correlated with conditions in which many animals in the spread school cannot see each other.

Finally, these patterns are stereotyped by species, and a trained observer can often visually identify the genera or species of dolphins by their aerial patterns, sometimes from long distances.

Perhaps the dolphins can make such identifications underwater by sound.

What can the use be of such sound signals? The following possibilities seem apparent: 1) If we can gage the activity state of a school by its aerial behavior, it is likely that the dolphins can do so too, and probably in a more refined way than we can; 2) such sound signals may be used where vision is useless; 3) school cohesiveness in the dark, or when animals are spread beyond the limits of vision, may be promoted by repeated short-range omnidirectional sound signals from all parts of a school. The incidence of aerial behavior is correlated with times when such signals would be most useful. This seems to us to be the most likely function.

We considered, and rejected the idea, that the spin might be a pattern relating to dominance or courtship in the school. This seems refuted because animals of all age classes and both sexes spin and because captive observations have shown that even animals that have been rejected from the social structure of a school spin.

Another possibility is that spinning is related to removal of ectoparasites such as remoras and copepods. While it might be useful occasionally in detaching such creatures, we have never seen a case in which this seemed to be occurring, and essentially every animal observed to spin was apparently without parasites. Captives spin regularly even though free of parasites.

THE DAILY ACTIVITY CYCLE

Observations of spinner dolphin schools along the Kona coast of the island of Hawaii, and to a minor extent elsewhere in the Hawaiian chain, show a regular sequence of activities during each 24-h period. Broadly, this consists of nighttime feeding, about which we know little, morning coastward movement that brings the animals into coves and sheltered coastline areas, rest, awakening, zigzag swimming, and then departure to the feeding grounds. Each of these activities will be discussed in turn.

Feeding

Feeding is upon scattering-layer organisms (Table 3) and seems to be performed during synchronous or subsynchronous dives of large and dispersed schools. What we take to be feeding dives start as early as dusk, before most of the scattering layer approaches the surface, and such evidence as we have (mainly from a single radiotracking, from chance encounters with schools at night, and from schools that we have followed to the feeding grounds) suggests that the schools patrol along the breaks in the submarine island slope and toward morning gradually make their way into shallow water over the shelf. A radiotracked animal, caught over approximately 140 m of water at Keahole Point just before dusk (at 1650 h) on 1 March 1971, moved back and forth along the shore between a point near Kailua-Kona and Kiholo Point. A detailed radiotrack was made during the night of 1-2 April (Figure 11). The animal stayed with a large school that moved slowly offshore and by 2000 was over the island slope. The group then patrolled back and forth over the slope within a stretch of coast approximately 20 km in length and over water that varied from about 360

TABLE 3.—Squid and shrimp in the diet of Hawaiian spinner dolphins.

Sample and date	Capture locality	Squid	Shrimp
0I70-42 Sept. 24, 1970	1 km off Ala Wai, Oahu	28 mantles (mantle length 25-52 mm, mean 38.9 mm) 5 *Abralia astrosticta* 14 *Abralia trigonura* 67 squid beaks, probably of the same species	11 pasiphaeids (to 17.8 mm carapace length) 1 small 4 abdominal portions 1caridean cephalothorax Probable euphausid fragments
0I70-35 Mar. 25, 1970	Off Waikiki, Oahu	2 *Abralia astrosticta* 7 *Abralia trigonura* 152 squid beaks of the above species 49 macerated squid	No identifiable remains
0I71-1 Jan. 8, 1971	200 m off Kailua-Kona Harbor, Hawaii	2 *Abralia astrosticta* 6 *Abralia trigonura* 204 squid beaks, probably of the above species 1 *Histioteuthis* sp.	20 *Sergia fulgens* (12.5-15.5 mm carapace length, mean 14.6 mm)
0I71-2 Jan. 8, 1971	200 m off Kailua-Kona Harbor, Hawaii	2 *Abralia astrosticta* 8 *Abralia trigonura* 310 squid beaks of the above species	1 *Acanthephyra* sp. 1 *Pasiphaea* sp. 2 *Pasiphaea* sp. 15 *Sergia fulgens* (12-14.5 mm mean 13.6 mm. Some of the above may be of undetermined species) 1 *Oplophorus grimaldii* (identification probable) 3 *Acanthephyra* sp. (identification probable)

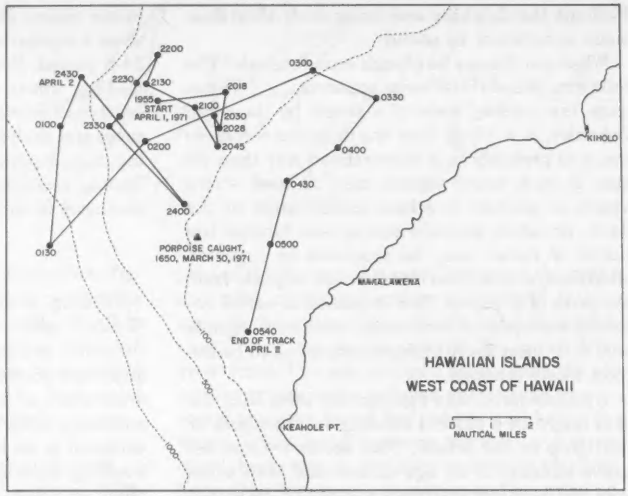

FIGURE 11.—Radiotrack chart of a marked spinner dolphin, 31 March-2 April 1971. Dolphin stayed in moving school of 100 animals presumably feeding over the island's submarine slopes.

to 2,600 m deep. By 0300 the school and the radiotagged animal had moved closer to shore and continued to move in ever shallower water until dawn.

Feeding schools were observed on three occasions at dusk. Each was composed of widely scattered groups, covering as much as 3 km in widest dimension, moving together. Diving was subsynchronous. Before a dive occurred, groups were evident and there was much aerial behavior across the entire width of the school. Then groups of the school dove individually, all following within approximately a minute or two. Dives were long, averaging 3.5 min according to our records. Surfacing was approximately as coordinated as diving; that is, the various groups straggled to the surface over a minute or two.

It was striking to see these very broad diffuse schools reverse their course in relative synchrony (within a minute or two), even at dusk, indicating a communication mechanism, probably acoustic, that could pass information rather quickly across the school.

Stomach contents were obtained from four spinner dolphins caught early in the day (before noon), while three animals taken in the afternoon had empty stomachs. This same pattern seems to occur in the oceanic spinner dolphins of the tropical Pacific, and a high percentage (65.3%) of empty stomachs (not segregated according to time of day) from 49 spinner dolphins taken from the eastern tropical Pacific were empty (Perrin et al. 1973). A time-stratified sample would probably show some food in the stomachs in the morning before digestion of the night's catch is complete, with empty stomachs in the afternoon. If spinner dolphins were diurnal feeders, one would expect few empty stomachs during the day at any time. The observed morning defecation period also fits this scheme. We conclude from our own observational data that the spinner dolphin in the open eastern tropical Pacific and around the Hawaiian Islands feeds at night. Our evidence, and that from other studies, suggests that it feeds upon scattering-layer organisms found at considerable depth. Fitch and Brownell (1968) reach a similar conclusion from otolith studies of stomach contents of five spinner dolphins taken from the yellowfin tuna grounds; they stated: "We feel certain that three of the cetaceans we investigated (*Kogia simus, Stenella longirostris,* and *Lissodephis borealis*) had been feeding 800 ft (250 m) or more beneath the surface . . . ." Perrin et al. (1973) similarly concluded that spinner dolphins are feeding mostly on mesopelagic fish and squid, with a small increment of epipelagic squid species in their diet. Our results (Table 3) confirm these earlier works, but show a considerable component of sergestid crustaceans in the diet of the Hawaiian spinner dolphin. Epipelagic squid were absent, though common in Hawaiian waters, while such relatively deepwater forms as *Abralia astrosticta*

and *A. trigonura* were common in the stomach samples but rare in collections of squid from Hawaiian waters. Richard Young[6] described *A. trigonura* as being uncommonly taken in Hawaii, but being a vertical migrant occuring from 500 m depth during the day to the upper 100 m at night. This species made up the majority of our samples. As for *A. astrosticta*, Young stated that it is known in Hawaii from only a few captures, and that most were taken on the bottom in trawls, while small individuals were sometimes taken in midwater. Our samples were adults. Young commented as follows: "It is a displaced midwater faunal element, or an animal having the distinctive adaptations of a midwater animal but which seems to migrate along the bottom. The *Histioteuthis* is also a vertical migrator that stays below about 150 meters." (See Table 3). John Walters (see footnote 6) commented that the shrimp *Sergia fulgens* is an enigmatic form known only in the adult form (ours were adults) from night tows.

Morning Shoreward Movement

After nighttime feeding, spinner dolphin schools turn toward shore, ultimately congregate in certain sheltered locations where the schools subside into the rest pattern. In the case of the radiotracked animal, this movement toward shore seemed to begin at about 0300 and to consist of a gradual movement that zigzagged ever closer to shore.

The directions from which schools come into Kealakekua Bay suggest that the movement toward the coast may be a general one and not necessarily pointed precisely at a rest cove. Some entering schools first swim along the coast, round Palemano Point at the south tip of the bay, and enter the bay over the shallows near Keei and Napoopoo (Figure 1), while others enter the bay directly from the open sea, coming in at various angles to the trend of the coast. Still others enter from the north, once again after a traverse of unknown length along the shore to the north of the bay. More schools enter along the southern limb of the bay than from the north or center. The true figure for south entry may be even higher than the figures indicate (58% for south entry vs. 14.5% for north entry; 27.5% entered in the middle sector), since some first sightings were made close to the cliffs at the back of Kealakekua Bay and, because of their location, were placed in the second sector records. It is likely that some of the schools entered from the south or north prior to the beginning of observation.

These congregation patterns suggest that the bays and coves used for rest periods may not necessarily be the direct target of daily inshore movement. The bays seem simply to collect schools that accumulate along the coast after a night's feeding. The fact that more schools arrive from the south than from the north may reflect the nearby presence of adequate resting areas over the rather extensive shallow-water areas immediately north of the bay between Keikiwaha Point and Keauhou. Waters to the south of Kealakekua Bay are deep close to shore and only very modest sized shallow coves exist at Honaunau and Hookena. Farther south, along the 20 km stretch of coast between Hookena and Milolii, no spinner dolphins were seen although both flights and ship searches were made. Nonetheless, data from marked animals show movement between the populations on each side of this gap. Unless rest areas are encountered, dolphin schools remain transient. This does not preclude the possibility that the animals may be familiar with the various rest coves or actively seek them when nearby.

Arrival times (Figure 12) concentrated between 0600 and 0950 h, though some schools arrived much later in the day. The early arrivals typically subsided into rest and spent the majority of the day in the bay. Later arrivals (those entering between 1100 and 1700 h) tended not to form resting schools and often moved out of the bay after a brief stay. The late afternoon arrivals may have completed a rest period elsewhere and then entered the bay as part of a longshore movement prior to going to the feeding grounds. Dolphins engaged in such longshore movements have been followed out to sea. In one such case a school rested, left the bay to the south, traveled slowly very close to shore until the small cove at Honaunau was encountered, and then turned out to sea as dusk approached.

Not all dolphin schools encountering Kealakekua Bay enter it. We occasionally saw schools crossing the bay mouth and swimming on in either direction. Our impression is that this occurred when other schools were deep in the bay, but unfortunately, adequate records to document

[6]Richard Young (Professor of Oceanography, University of Hawaii) examined and identified stomach samples from our Hawaiian spinner porpoise in 1973 and provided notes on the occurrence of squids in the samples, while John Walters (University of Hawaii) provided identifications of shrimps.

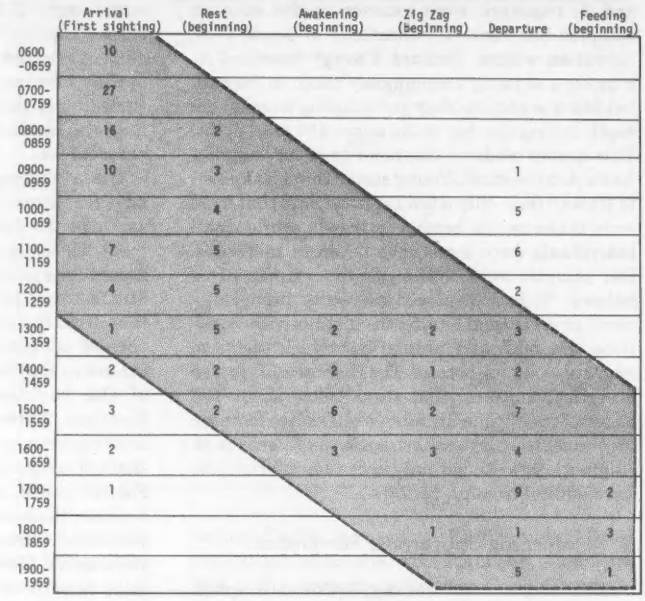

FIGURE 12—Cumulative record of time of first sighting, onset of rest, wakening, etc.

the point were not kept. Our efforts at listening to dolphins in Kealakekua Bay showed that dolphins at the mouth of the bay can easily hear those in its deepest recesses, so the effect may be one of exclusion of the passing school by occupants. The point needs further study.

Small schools often seemed to coalesce upon arrival in the bay. This first became apparent when our estimates of school size during an arrival sequence increased sharply, or even doubled, between the time the animals were at the bay entrance and when they were deeper in the bay. In other records such obvious increase in school size occurred after the animals were deep in the bay. The arrival of such supplementary schools was occasionally observed and their coalescence into a single school noted.

School structure during entry was best observed in those that entered in the central sector, without the visual interference of headlands or the swells and breakers that sometimes obscured sightings close to shore. Such schools were sometimes first seen as far as 4 km beyond the bay and could be watched during the entire entry traverse. These schools typically swam in a ragged rank composed of quite discrete groups. The dolphins were often quite active, and their passage was accompanied by spins and other aerial behavior. Often, by the time the bay mouth was reached aerial behavior had subsided considerably, though it often persisted to some degree for as long as 2 h after initial entry. In small schools of approximately 6-15 animals, entry was often quite unobtrusive. In spite of a conscientious watch from the clifftop during early morning hours such small schools were sometimes seen first deep in the bay. Large schools typically exhibited more aerial activity than small ones, and it appeared to persist for a longer period.

Arriving dolphin schools often come to the bows of vessels where they engage in assisted locomotion or "bowriding" (Norris and Prescott 1961). Even so, if a vessel pursued such schools, repeatedly making passes through their ranks or changing speeds upon approach, the school usually edged toward deep water, and if the harassment continued, the school left the bay. Observers on shipboard usually failed to note the effect on the school as a whole, since their attention was focused on the bowriding animals. But an observer on the cliff above the bay, watching the entire school, could quickly discern this retreat. This effect nearly always occurred, even if the intruding vessel moved very carefully. Later, when the school had subsided into quiescence, it was much

more difficult to disturb the animals sufficiently to cause them to flee the bay. Even persistent attempts to enter their ranks merely caused avoidance and often a transitory flurry of aerial activity (Figure 13).

Defecation was a common feature of arriving schools, prior to subsidence into rest. From the underwater viewing vehicle the olive colored trails of semiliquid fecal material were often seen streaming from the dolphins. Three or four animals sometimes defecated simultaneously within the field of view of the vehicle. A rate for one 40-animal school was calculated at one defecation every 15 s. Presumably this rather short defecation period is related to nighttime feeding and early morning digestion. The trailing animals of a school swam through the dispersed clouds of feces with no evident reaction.

Subsidence Into Rest

Once a spinner dolphin school arrives deep in Kealakekua Bay, it normally subsides slowly into rest, a process sometimes requiring 2 h or more. This process is so gradual and so affected by features such as school size and the time of day, that its precise onset was difficult to assign (Figure 13), and an arbitrary definition was necessary. Because rest involves the cessation of aerial behavior by all school members, we defined rest as occurring when a 10-min observation of the school revealed no aerial behavior. Occasionally, even this criterion was confounded because aerial behavior is, to some extent, "infectious," and a school subsiding into rest may sometimes exhibit 10-min periods without aerial behavior followed by periods in which some aerial activity occurs in several animals. But, generally, once a school was quiet for 10 min, little or no aerial activity occurred until arousal. Typically arriving schools were in ranked form, with group structure evident. Such schools often moved quickly (5-8 km/h) and swam resolutely, with considerable aerial behavior. Little time was spent below the surface. Dives were brief (Figure 14). Once such a school arrived at the back of the bay, under the lava cliffs,

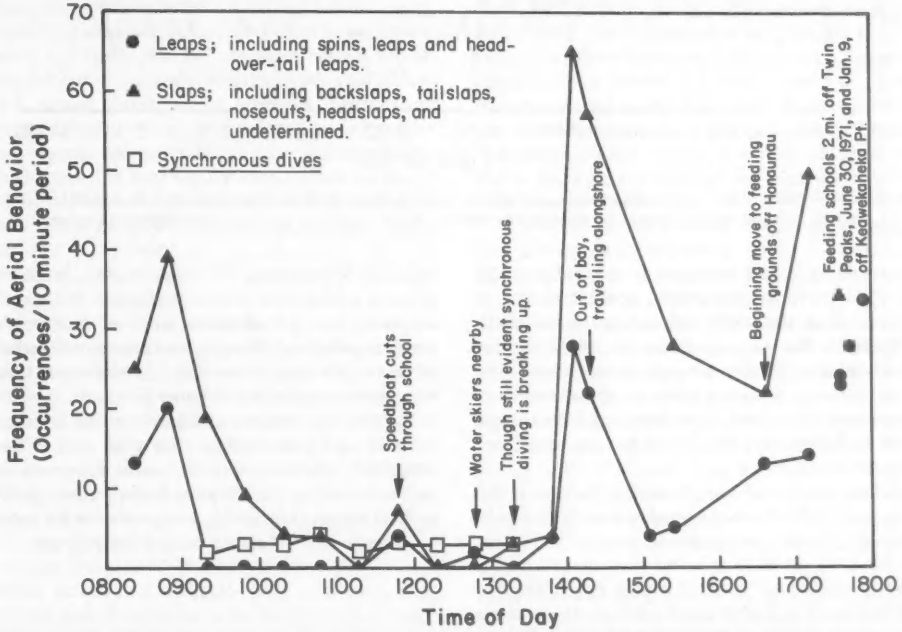
Leaps; including spins, leaps and head-over-tail leaps.
Slaps; including backslaps, tailslaps, noseouts, headslaps, and undetermined.
Synchronous dives
Frequency of Aerial Behavior (Occurrences/10 minute period)
Time of Day
Speedboat cuts through school
Water skiers nearby
Though still evident synchronous diving is breaking up.
Out of bay, travelling alongshore
Beginning move to feeding grounds off Honaunau
Feeding schools 2 mi. off Twin Peaks, June 30, 1971, and Jan. 9, off Keawekaheka Pt.

FIGURE 13.—Aerial behavior per 10-min interval for a spinner dolphin school of approximately 40 animals, 30 June 1971, Kealakekua Bay, Hawaii. Synchronous dives define the rest period, broken briefly by the speedboat. See text.

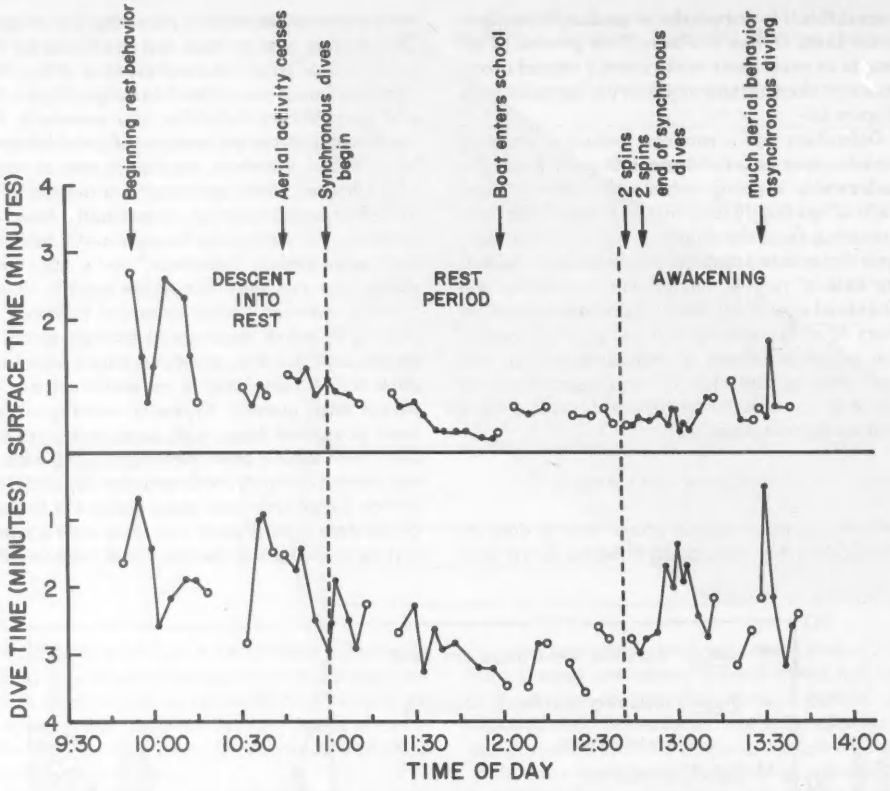

FIGURE 14.—Trends in diving and surface times in a 40 animal school of spinner dolphins, Kealakekua Bay, Hawaii, 2 May 1970. Breaks in record represent loss of the school by the observer, when a surfacing and descent was apparently missed.

it moved back and forth across the width of the bay. Its traverses sometimes took it nearly to Kaawaloa on the north and to Keei on the south (Figure 1). The various classes of aerial behavior slowly disappeared in a rough graded series: the most athletic patterns such as spins and tail-over-head leaps first, then head- and backslaps, then tailslaps, and finally all but an occasional noseout was gone.

School size and shape gradually changed at the same time. The ranked school shifted into a subdiscoidal shape and tightened markedly. For instance a school of 30 animals that once formed a spread rank over 75 m of water might become concentrated in a 20 m diameter disc. Movements became leisurely; in fact, the surface excursions of the schools became almost surreptitious as the animals rose quietly from the depths, breathed once or twice, and descended again. It became very easy to overlook them, and two or three observers were needed to produce a complete record of their dive sequences. During rest most time was spent underwater (Figure 14).

Vocalization was at a high level in arriving schools and subsided as the rest period approached. Arriving schools made a variety of noises including click trains, burst pulse signals such as squawks or barks, and pure-tone whistles or squeals. All but clicks ceased during rest.

Rest

During rest, quiet spinner dolphin schools moved slowly back and forth, deep in the bay.

Their excursions were entirely confined to shallow water (about 3-50 m). Only when disturbed or when rest was over did the schools begin to edge into deeper water. For instance, resting schools seldom ventured into the deep channel that entered the bay at Kaawaloa, but instead moved mostly back and forth between our observation station #1 and Napoopoo (Figure 1), an area of shallow sandy bottom dotted here and there with isolated coral heads.

Resting schools often changed direction underwater, which made it difficult to predict where they would surface. Interindividual and intergroup distances gradually decreased as rest deepened, until many animals were very close to or actually touching one another, while the arriving school showed evident group structure and independence of both movement and diving time within the school; the resting school swam in much closer synchrony. Arrival of synchronous diving by an entire school provided a good, if arbitrary, indicator of the onset of rest.

On a few occasions we were able to watch synchronous dives from the MOC. The underwater vantage point allowed the observer to see subgroups of animals in the school as a whole. Tight, uniformly oriented groups dove slowly, with measured tail beats, toward the sand bottom below; leveled out a few body lengths above the bottom and moved slowly along, schooled tightly; and swam largely without individual exploratory movements. Occasionally an animal descended to the bottom and beat boils of sand up into the water with its flukes. At the end of a dive the animals rose rather steeply to the surface, not as a single tightly integrated group, but more or less seriatum, as a column of subgroups. Often after rising, the animals spread outward from this rising column a short distance before turning to define the compact confines of the surface school, like the petals of a flower opening. Once on the surface, group structure could be seen, but the animals seemed much more regularly spaced than is the case in active schools. Diving, too, was steeper and slower than in travelling groups. While individuals in resting schools seemed less alert than animals in feeding or travelling schools, the resting school itself was very wary of strange features of its environment. Any strange object placed in a rest cove, such as a buoy, boat, or line was avoided for a matter of days before a school seemed to habituate to its presence. It was striking that they reacted to foreign objects in much the same way as we have come to expect from fish schools, and not with typical dolphin individuality. For instance, when a resting school cruised inshore of us near the cliffs, we waited in a quietly rocking skiff some 75 m offshore, and the school approached slowly as a discoidal group, thinned as it reached a point directly inshore of us, streamed betweeen the skiff and the cliff as a long line of quietly moving animals, and reformed its discoidal group once past us. We found that our skiff or our anchored workboat could deform such discoidal groups from some distance, causing the side nearest the skiff to become dented or malformed as the entire school reacted to our presence. When a four-hydrophone array capable of sound triangulation was placed near the path of such resting schools, it was assiduously avoided and no animals were known to pass through it for 6 days after its placement (Watkins and Schevill 1974). A line stretched across the surface of the water was capable of deflecting such schools. In such cases, even though the animals moved slowly and other evidence of alertness, such as complex phonation or aerial behavior, was nearly absent, the school as a whole remained alert. We suppose this is due to sensory integration by the closely packed school, that is, by the reception of environmental information by some members of a school and transmission of its occurrence to all or most of them. It was usually possible to cruise among alert schools, and many individuals might station at the bow within a few feet of an observer, but resting animals very seldom came to a vessel.

A graphic demonstration of spinner dolphin's fear of strange objects was given by our attempts to encircle quiescent spinner dolphin schools with a modified Hawaiian "hukilau[7]."

Our hope was that this fear might be utilized to assist in their release from tuna seines, since at the time large numbers were being killed per year in the yellowfin tuna fishery. We conceived that light weight gear of this sort could be deployed in a tuna net to crowd the captive animals, and thus assist in their release. Our tests, run in August 1973 in Kealakekua Bay, used a hukilau composed of 450 m polyporpylene cork line (½ in; 1.27 cm) from which were hung every 2 m, thin poly-

[7]A hukilau is a Hawaiian "net" made of a cork line with palm fronds woven through it at intervals, which is towed across coral areas, chasing fish in front of it. Because a mesh net is not involved, it does not entangle on the rough bottom but still serves to concentrate the fish, which are then netted from inside the hukilau over sandy bottom.

prophylene lines (¼ in; 0.6 cm) 18 m long (Figure 15). With this insubstantial barrier we were able to encircle whole schools of spinner dolphins in 20-40 m of water and to crowd them severely. In one case when the hukilau was reduced to a surface area of 6 × 10 m, a school of 40-60 animals refused to leave through the wide openings but continued to mill inside (Figure 15). Even when two of the thin vertical lines were removed, leaving a "door" 6 m wide, the school continued to circle, "eyeing" the opening but not passing through it. Only when the area was further reduced did the majority of the animals pass through the wide opening. They had been held captive for 3 h 50 min in this fashion.

Although large and small schools may become quiescent, sporadic low intensity aerial behavior may continue. The impression given is that very small schools (ca. 6-12 animals) maintain a degree of individual wariness, perhaps related to the uncertain protective effectiveness of their few members, while very large schools may always contain some alert animals. For instance, based on a small number of observations in the large (100-150 animals) schools seen at Keahole Point, we have never noted deep quiescence. It is as if the members of the small school were afraid, and that some activity always occurred somewhere in the larger schools. Only schools of about 20-40 animals seem to achieve the most complete quiescence.

Even though aspects of diurnal behavior sequences were recorded on 83 days, complete sequences were recorded on only 13 days. Based on these observations, rest periods ranged from 41 min to 6 h (mean = 3.62 h).

Once quiescent, resting schools are rather difficult to disrupt. Several times cruise boats or water skiers went through resting schools during our observations. The usual result was a brief flurry of low-level aerial behavior, for example, a desultory headslap, an imperfect spin, and then the school would subside into complete quiescence again (Figure 13).

Arousal

Arousal, unlike descent into rest, is abrupt, both in terms of school dispersion and aerial activity. In a completely quiescent spinner dolphin school, arousal was marked by sudden active aerial behavior—a complete spin or headslap, for instance. Within 10 min of such initial aerial activity the school was often fully alert, with aerial activity high throughout the school. In fact, the highest levels of aerial activity recorded occurred at arousal, and later, during feeding (Figure 13).

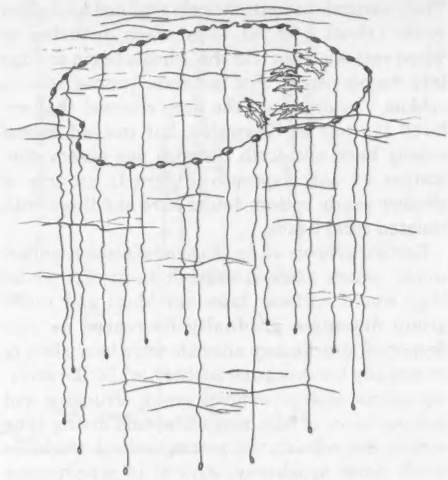

FIGURE 15.—An Hawaiian "hukilau" composed of a cork line and hanging vertical weighted lines, showing a school of spinner dolphins held inside. Vertical lines are 3 m apart and 20 m long. See text.

Zigzag Swimming

At arousal the pace of the spinner school quickens. Group structure suddenly becomes obvious again. At arousal the school moved back and forth across the bay, or sometimes in and out from the bay center to the cliff base. In either case the school often began to traverse deep water. Typically, it swam toward the bay mouth beginning with a flurry of activity and speed, often with animals rushing through the water, creating spray and small bow waves as they raced along. As the bay mouth was approached, usually the school gradually slowed and finally began to mill then turned back into the bay. Sometimes the school then subsided into further rest, or accelerated again, often toward the opposite side of the bay. This entire pattern is what we have termed "zigzag" swimming. These patterns, we suspect, are, to some extent, influenced by the topography of Kealakekua Bay, and may take somewhat different expressions elsewhere.

Spinner dolphins were observed moving in zigzag fashion at Kealakekua Bay, in and out and from headland to headland. The longest bout of

this behavior took 2.75 h. Typically zigzag swimming ended with fast swimming that took the school beyond the confines of the bay altogether. It was as if one had been rocking a blob of mercury in a bowl, and a final strong motion sent the blob flying, completely free of the bowl.

If the animals left the bay early in the day, the school usually traveled close to the shoreline, either to the north or south, and later in the day, turned toward deep water offshore. When a school left the bay near dusk, it usually headed directly out to sea.

As exodus from the rest location began, schools traveled either as ranked schools (wider than long) or in straggling lines arranged in more or less linear fashion. As the school moved offshore, it spread. It sometimes coalesced with other schools moving in the same general direction. By the time feeding grounds were reached, usually near dusk, a school that, during rest, had formed a 25 m diameter disc might have expanded until its groups were scattered over a kilometer or more of sea. As noted earlier, we have estimated some feeding schools as 3 km in breadth.

Social behavior, including mating, aerial behavior, sexual play, and aggressive chases, becomes especially evident in spinner dolphin schools moving toward the feeding grounds. Once there subsynchronus feeding dives begin.

Dive Patterns

An example of the daily cycle of dive patterns is shown in Figure 14. As animals entered the rest area, the pattern was one of short dives, with most time spent on the surface. Then this pattern gradually shifted as dives became longer and surface times shorter. When the school was near or over the shallow area where rest occurs, dives become synchronous, or nearly so. During arrival the groups of a school, especially if it was a large one, often dive out of synchrony with one another. During rest, as shown in Figure 14, the duration of dives continued to increase until the longest dives were approximately 3.5 min duration; surfacings at that time were brief, between 10 and 30 s duration. Throughout the rest period, the school, if it is small or moderate in size, dives in synchrony. During the arousal period, surface times gradually increase while dives tend to become much more variable in length than during rest. Finally, as the school travels out to sea, individualism reaches its peak, with animals scattered in pairs or small subgroups, or even alone, within the envelope of the school as a whole. Synchronous diving is lost as movement is at or close to the surface and directed into horizontal travel. Then, on the feeding grounds, when the school is at its most dispersed, the scattered school slows and begins synchronized diving again, presumably to feed. Internal factors, such as the return to equilibrium after a dive might play an important role in determining diving patterns. As for mediating signals, the cessation of aerial behavior in an area of the school that has dived could signal adjacent school segments that diving is occurring; or, vocal signals could mediate it, and thus a wave of information about a dive in progress could travel across the school. The high incidence of aerial behavior in feeding schools and the lack of precise synchrony in feeding dives support such a speculation.

Social Behavior

Social behavior in wild spinner dolphin schools has thus far proved all but impossible to observe in an orderly fashion. Glimpses of individual animals or subgroups are fleeting, and the opportunity to identify individuals or their sex is sporadic. Hence, the observations that follow are highly fragmentary.

Mother-Young Behavior

Very small calves are always seen in the company of adults. However, young spinner dolphins of quite small size (about 1.2-1.7 m TL) may form groups within a school with no evident adults in close attendance. Newborn calves with adults have been seen at all seasons of the year (Figure 16), as have groups of unattended larger calves.

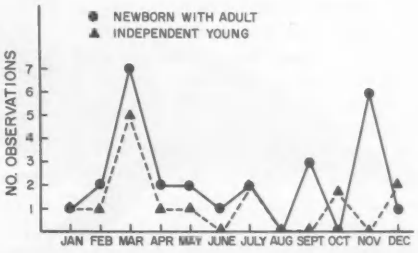

FIGURE 16.—Annual occurrence of newborn in spinner dolphin schools off Hawaii (1968-72). Only sightings of newborn with evident fetal folds are included.

Nursing has seldom been seen in nature. In one clifftop observation, a 60-animal school swam below, containing a group of adult-calf pairs. One of these pairs engaged in nursing. The adult turned slightly on her side as the young dolphin positioned itself obliquely alongside with its beak pressing against her at the mammary slits. The behavior persisted for a few seconds before the animals dove. The posture was like that reported in captive dolphins (Dohl et al. 1974).

For 33 days in February-March 1970, a female pair was seen in Kealakekua Bay and nearby Keauhou. Unlike most such pairs, the two often swam near our observation vehicle. The calf had the distal 5-6 cm of its rostrum broken through and bent to the side with some ragged flesh exposed. In spited of this apparently grievous wound the calf appeared active and well nourished. Contact was very frequent between mother and calf. Both the adult and calf used their flukes, flippers, and dorsal fin to achieve this contact. On two occasions the young animal touched its dorsal fin to the adult's flank, laid its flukes up under and touching hers, and held this position as their combined tail beat propelled them both along. The young animal rode both above and below the adult, sometimes directly beneath her midbelly, occasionally sliding backward until the moving flukes of the adult tapped against its dorsal fin. In our observations we never noted true assisted locomotion as described by Norris and Prescott (1961), though swimming speed was generally so slow that it might not be expected.

A common posture was for the baby to swim below and a little to the side of the big female, at which time she placed her flipper against the young animal's back, just anterior to its dorsal fin. Much of the time the pair in this position swam in synchrony, turning and diving together.

On occasion the young animal swung away from the adult for a few meters but soon turned, increased speed, and rushed back to her. Once, during a particularly long sortie, the adult pursued the calf, slapped its back with her flukes, and then the pair dove together.

Sexual Associations

At times, both on a given day and over several days time, specific subgroups of 2-6 spinner dolphins whose members could be individually recognized, were seen together from the viewing capsule. It was possible to determine the sex of some of the animals. Sexually related behavior was exhibited between male and male and male and female pairs. It takes several forms. What Bateson (see footnote 5) called "beak propulsion" was noted (Figure 17). In it one animal swam up from below another and inserted the tip of its rostrum into the genital slit of the upper animal, apparently pushing the passive animal along. Both the dorsal fin and the flippers are commonly used to stroke or

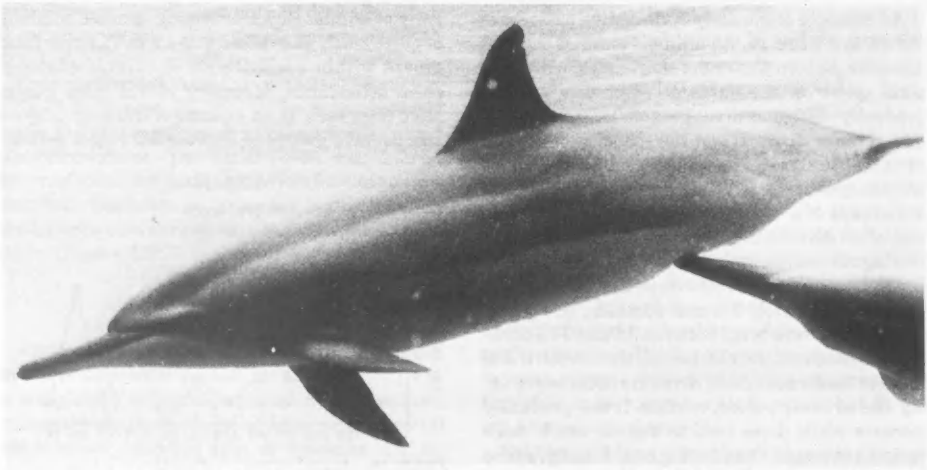

FIGURE 17.—Beak propulsion by a captive pair of spinner dolphins at Sea Life Park, Hawaii. An adult female is pushing an adult male.

probe the genital area of another animal, and the upper animal sometimes rode along with the dorsal fin of the lower animal pressed into its genital area. Mating postures were commonly seen, most often in alert schools early in the morning or near dusk. On one occasion (in captivity) we were able to determine that both partners in such a pair were males, even though females were present in the tank. We were able to confirm heterosexual contact in some pairs in nature. Typically, one animal swam in the normal upright orientation while another swam upside down, with the genital areas of the two pressed together. Either sex could be above or below. Intromission was usually difficult to see, but was noted on occasion. Contact was sometimes maintained for several seconds. In some observations the upper partner was relatively quiescent and propelled itself with fluke strokes of much reduced amplitude compared with those of normal swimming. One mating chase was noted as a school moved onto the feeding grounds off Keauhou, the pair raced by the bow of our vessel as we travelled at an estimated 4 kn. They dove and spiralled swiftly together. The coupling and synchrony of movement of the pair was so perfect that the two animals were not evident until the pair turned on its side. Together they veered away from the bow, diving about 20 m down and remaining in the coupled position for several seconds. We heard whistling with the unaided ear when such coupled animals were near the ship.

A particularly complete observation of mating was made from the MOC on 26 July 1970, at Kealakekua Bay. A male-female pair swam directly in front of the viewing capsule, and the female swung under the male until their ventral surfaces were in contact. The penis of the male was seen to enter the female, though no thrusts were noted as the position was held for 3-5 s, while the animals glided without fluke strokes, and then the animals parted. Shortly, the female again moved under the male, but no further intromission appeared to take place. Instead, the male accelerated with a few fluke strokes, and the pair cruised off, side by side.

Competition for partners was occasionally observed. On 29 March 1970 at Kealakekua Bay, the MOC entered a school of 12-13 animals, and 2 were noted swimming upside down. Both pursued and came up under a single adult above them. Later, three inverted animals pursued two in the normal swimming posture. At that moment another large adult swam rapidly to the moving group and forcefully inserted itself between one inverted animal and the one above it. The upper animal then dove away from the group, with the intruder following. The two inverted animals moved quietly, maintaining their upside-down orientation, toward another nearby animal swimming in normal orientation.

Observations of captive spinner dolphins show that much social interaction is sexually related and that it may occur between animals of all age classes and combinations of both sexes. As has been found in the Atlantic bottlenose dolphin, *Tursiops truncatus*, sexual behavior and social communication are interwoven to such an extent that it is often impossible to separate true courtship and mating behavior from communicative behavior of other sorts. For example, Caldwell and Caldwell (1967) reported a 2-day-old male Atlantic bottlenose dolphin having an erection when brushed by its mother. Sexual maturity is not reached in the spinner dolphin until a minimum of 3.7 yr (Perrin et al.[8]) and even later in the bottlenose dolphin, and thus one must view this precocious use of sexual patterns as part of the development of communication concerning relationship. Such communicative use of sexual patterns has been reported for mixed schools of captive spinner and spotted dolphins (Bateson see footnote 5).

Other Social Patterns

Contact, not necessarily sexual in context, is common between members of dolphin schools. When groups of animals swam near the viewing capsule, one could often see animals touching one another with the tips of pectoral fins, the dorsal fins, or fluke tips. Jostling or pushing of animals near the capsule often occurred and was accompanied by sound emissions. Such jostling can be seen commonly in other bowriding groups. Because a few animals from a given school seem to do most of the riding and some seem to occupy specific places at the bow, one gains the impression that hierarchical relations in the school are involved.

The release of air may correlate with social signals in spinner schools. Commonly, long streams

[8]Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Growth and reproduction of the eastern spinner dolphin. A geographical form of *Stenella longirostris* in the eastern tropical Pacific. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Admin. Rep. LJ-76-13, 84 p.

of air were noted issuing from the blowhole corners in spinners near the capsule. Whistles and chirps could often be heard concurrently. Sometimes, during active chases one or more animals would release a large bubble of air underwater, which boiled upward to the surface. Pryor (1973) has correlated such behavior in captive animals with frustration.

Spinner dolphins change school swimming patterns in relation to weather. In rough seas, groups of dolphins appear to ride the swells and breaking waves that sweep toward the Kona coast. On one such occasion, while we "hove to" in a rough sea, perhaps 100 spinners passed us. They were divided into small groups of less than a dozen animals. These groups swam tightly together and often could be seen racing down the foreslope of the waves, sometimes breaking the water together and sometimes staying wholly within the wave. Such behavior is commonly seen in other cetacean species (Norris and Dohl in press).

Sound Emmissions

A detailed study of spinner dolphin sound emissions will be presented in a future paper. A few observations are appropriate here.

There is a marked diurnal fluctuation in the kind and amount of spinner dolphin vocalization (Powell 1967). Alert schools produce an array of sound types such as clicks, pure-tone whistles or "squeals," and a variety of burst pulse signals that can be described by such terms as barks, moos, chirps, etc. The clicks are of considerably lower intensity than either the whistles or the burst signals (Watkins and Schevill 1974), and the clicks may be more tightly focused.

Resting schools are nearly silent, emitting almost entirely clicks and even these are sporadic. Simultaneous with arousal, vocalizations rise in variety and abundance. Whistles and burst pulse signals can be heard quite long distances underwater. With Watkins and Schevill, we were able to station ourselves outside Kealakekua Bay and hear whistles and various burst pulse signals from a group of spinners swimming close to the cliff, approximately 2 km distant. Thus, a school of dolphins swimming outside Kealakekua Bay during longshore movement would be able to detect animals deep in the bay without entering it. It is possible that the schools we have seen passing the bay when others occupied it may have been excluded by acoustic signals.

No context-specific sound signals have been identified by us, except that it seemed clear that clicks were emitted concurrent with the inspection of the environment. The likelihood of context-specific acoustic signaling in the daily events in the school, however, seemed high. For example, synchronous diving in very widely dispersed schools, or simultaneous turning of an entire school at dusk, are unlikely to be visually cued (though it is not impossible). The sounds produced by aerial behavior have, in a few instances, been picked up by our listening gear. Tailslaps are especially loud, while spins (which we have recorded in captive situations) produced a lower intensity signal quite different in character.

Predators

Hawaiian spinner dolphins seem to be attacked with some frequency by sharks. Several of the scarred animals we cataloged had obviously been wounded by large sharks. Lunate rows of tooth marks, especially on the tail region, some apparently from sharks with a 12-15 in (31-38 cm) gape were noted. In one case it seemed that the entire tailstock had once been in a shark's mouth. Nicked or tattered dorsal fins may also have been produced by shark bite.

Subcircular scars somewhat larger than a silver dollar commonly seen on tropical and subtropical cetaceans are common on spinner dolphins. Jones (1971) suggested that these scars are produced by the small squaloid shark *Isistius brasiliensis*. This small shark occurs with scattering layer organisms, is bioluminescent over its entire body, and is thought to be a squid mimic. Feeding dolphins may be attracted to it, and when close, the shark may swim to the dolphin, attach itself, and then scoop out a disc of blubber and flesh with its peculiar dental and branchiostegal apparatus. The shark has erect cutting teeth only in the lower jaw and a jaw apparatus that allows it to attach and push the teeth through the flesh of its prey like a cookie cutter. The shark may bite while facing the tail of the porpoise and be swung around in the current, cutting as it goes. Discs of dolphin blubber have been found in the stomachs of this shark (Jones 1971). We have seen fresh wounds of this shape and size several times, including some completely through the blubber to the flesh beneath. Nearly every adult dolphin bears some scars of this sort, on some part of its body. We have never seen such scars on the appendages or head, though

they are common on the throat, flanks, and especially on the belly and the region between the flippers.

DISCUSSION

Instead of finding tightly knit schools of constant size that habitually occupied a given cove, as we had expected we found coves occupied by schools of highly variable numbers and composition. These variable schools often merged with other schools to form large feeding groups offshore, and school members moved back and forth between resting areas many kilometers apart in what seemed a completely free fashion. Rather than finding dolphins occupying a "home cove" the tendency to gather in shallow waters near shore seems to be related to a combination of topographic factors including the presence of adequate areas of shallow water and the proximity to nearby deepwater feeding grounds. Further, the population occupying such a cove during the daily rest period seems limited in some fashion by this same topography. Kealakekua Bay seems able to hold only about 60-70 animals, and even this number seems so large that rest may be inhibited. Deep rest, without aerial behavior, seems only to occur when relatively few animals, about 30-40 or less, are in the cove. In contrast, Keahole Point regularly holds >100 animals during daily rest.

Instead of finding schools headed directly for rest areas in the morning, we found schools moving toward the coast in the morning in a much more general fashion, encountering the coast, swimming alongshore, entering coves, sometimes coalescing with schools already in occupancy, or apparently sometimes passing by a cove filled with animals, to move on toward other less occupied rest areas. The entry and exit patterns of schools relative to coves also suggests such opportunistic use. At Kealakekua Bay, schools entered primarily from the south perhaps because rest areas south of this bay are very restricted while much more extensive areas exist to the north and in effect this inhospitable shore "collects" but does not hold incoming schools, Exit, on the other hand, is primarily to the north, as if schools came into the cove rested for a time, and continued on their way toward offshore feeding grounds. The primary feeding grounds seem to be to the north and west of Kealakekua Bay, off the shallows of the island, though our observations are sparse. To the north of Kealakekua Bay are other rest areas, while to the south deep water adjoins the shore. Thus occupancy or lack of same of a given rest cove and arrival direction to it may be related to nighttime feeding movements which leave animals offshore at various locations after the scattering layer descends with dawn. None of this, of course, indicates that dolphins do not know where available rest areas are, or know the features of them.

What, then, is the true dolphin school? Are the large offshore aggregations, formed of a coalescence of smaller resting groups, such a cohesive unit? Or, should we focus our attention on school subgroups of a few animals, which may habitually swim together (though our evidence is inconclusive in this respect), in the search for structure, regarding the large groups as opportunistic assemblages? Or, can both be properly considered as schools?

The large offshore feeding assemblages have clear structure in some respects. Such schools often dive and surface more or less together, and much social behavior is evident at times in them. These schools swim in a common direction and sometimes change course in a coordinated fashion. We often noted age-related subgroups within them; mothers and calves, or juveniles swimming together. But, if such schools are followed, they will sometimes split into parts that move in different directions, and clearly, they fragment during the day when smaller schools enter coves or shallows to rest.

Smaller schools exhibit most of the same behavior, though many times not all age classes will be represented in them. Schools of less than about 30 animals are seldom split for long by a vessel. These groupings we call schools, preferring to recognize that such schools change in size from time to time.

Clearly, from our marked animal information, individuals utilize a rather extensive area of coast for feeding, moving from group to group, and thus, in aggregate the population of a given portion of coast is a functional unit, in relation to its trophic relations with the immediate environment. The degree of discreteness of such populations from those adjacent remains wholly unknown, as does any possible intermixing between islands.

Considering this high degree of fluidity, how is directed movement of a school achieved and how does the structure of schools come about? No leader seems to exist in the standard sense of an animal determining direction of movement by

swimming at the head of a group. Yet directed movement does occur in cetacean schools. Killer whales arrive off sea lion and sea elephant rookeries at the proper time to catch pups (Norris and Prescott 1961), and pilot whales arrive at specific feeding grounds when squid come to spawn or when capelin arrive in large schools (Sergeant and Fisher 1957). Such patterns presumably have a learned component, and similar patterns of dolphins opportunistically using human activities to locate and capture food must be largely or wholly learned. For instance, bottlenose dolphins follow trawlers in the Gulf of Mexico (Leatherwood 1975) and in the Gulf of California (Norris and Prescott 1961) and obtain fish and other food items stirred up by the trawl or cast over the side during sorting of the catch.

Tavolga and Essapian (1957) described adult male bottlenose dolphins harassing newborn calves and their mothers, and dominance by adult females is also discussed. We have noted strong aggressive behavior in captive male spinner dolphins at Sea Life Park oceanarium in Hawaii. In the wild dolphin school, similar actions probably serve to order the structure of the school. Females and newborn young may be herded to their normal position in the interior of the school. We expect that such aggression combined with experience may serve to regulate the direction of school movement from various locations in a school. For instance, adult male killer whales usually occupy a position in travelling schools far out on the wings of the moving group, and from this position directional signals may be communicated to the school as a whole (Norris and Dohl in press).

The tendency of spinner dolphins to rest over shallow sandy areas is most probably a protective adaption allowing the quiescent school to place a protective bottom close beneath it and a shore nearby on one flank. The chances of attack from those directions by large deepwater sharks are correspondingly reduced. With much individual behavioral flexibility suppressed in resting schools, collective wariness rises, we presume through sensory integration by the school. Thus, the use by spinner dolphins of alert daytime-feeding spotted dolphin schools in the open eastern tropical Pacific Ocean, we feel, may account for the otherwise unusual daytime association between these two species.

We regard this study as preliminary, allowing glimpses into the life of one wild dolphin species and focusing our attention on important problem areas such as acoustic signalling, school structure, energetics, and social relationships.

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Richard Young and John Walter of the University of Hawaii identified the cephalopod and shrimp remains in stomach contents.

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LARVAL DEVELOPMENT OF *HYPOCONCHA SABULOSA* (DECAPODA: DROMIIDAE)[1]

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ABSTRACT

Larval development of the dromiid crab, *Hypoconcha sabulosa*, consists of three zoeal stages and one megalopa. The zoea exhibit numerous characteristics normally associated with anomuran larvae.

Hypoconcha sabulosa (Herbst) is a relatively uncommon inhabitant of coastal waters from North Carolina to the coast of Texas. Another member of the genus, *H. arcuata* Stimpson, coexists throughout much of the range (Williams 1965). These crabs are frequently overlooked owing to their habit of carrying an empty clam shell on their back. Kircher (1970) described the laboratory-reared larval stages of *H. arcuata* the larval stages of *H. sabulosa* are undescribed.

The family Dromiidae is an enigmatic group which has remained a point of contention in the phylogeny of the Decapoda. It has often been suggested that the brachyurans are a monophyletic group and that the dromiids represent a primitive true crab (Balss and Gruner 1961; Glaessner 1969; Stevcic 1974; Warner 1977). However, it is also strongly argued that the brachyurans are polyphyletic and that the dromiids are more closely related to anomuran or thalassinid groups (Gurney 1942; Williamson 1974).

METHODS

On 14 June 1976, a single gravid *H. sabulosa* female was collected by dredging in the North Inlet estuary, near Georgetown, S.C. Water temperature at the time of collection was 24° C; salinity was 27‰. The female was returned to the Baruch Laboratory, Columbia, S.C., and placed in a 9 cm Carolina culture dish containing filtered natural seawater of 25‰ salinity and maintained at 25° C under a 14L:10D light schedule. On 21 June, the brood began hatching and 22 active larvae were placed individually in 6 cm dishes containing 15 ml filtered seawater (25‰) and maintained as described for the adult. Water was changed daily and freshly hatched brine shrimp nauplii (San Francisco Bay Brand[4]) were added as food following each water change. Additional larvae hatching during the following day were reared in a 1 l shallow glass dish under similar conditions. These larvae were sacrificed during development to provide replicate material for descriptions.

Records were kept for each of the 22 larvae individually cultured to determine the number and duration of larval stages. Exuviae and larvae were preserved in 70% ethyl alcohol. Drawings were made from preserved larvae using a Zeiss drawing tube. Measurements of preserved larvae were made with an ocular micrometer; total length and carapace length are as defined by Pike and Williamson (1960a). Abbreviations and setal types mentioned are as in Johns and Lang (1977). Descriptions and sizes are based on at least five apparently healthy larvae sacrificed at each stage.

RESULTS

Development

Three zoeal stages and a megalopa were obtained through laboratory rearing; no variability in the number of larval molts was observed. Larvae were easily reared in both mass culture and individual chambers. Of larvae not sacrificed, 72% survived to megalopa and 75% of the megalopae successfully molted to first crab (Table 1).

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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TABLE 1.—Survival, development time, and duration of the larval stages of *Hypoconcha sabulosa* reared in the laboratory.

Item	Zoea I	Zoea II	Zoea III	Megalopa	1st crab
Percent survival from first zoeal stage to successive stages (% based on original 22 minus those sacrificed for figures)		86	76	72	53
Percent survival within each stage (% of stage not sacrificed to reach subsequent stage)	86	89	93	75	
Days from hatching to reach each stage mean (range)		3.6 (3-6)	7.2 (6-9)	10.5 (9-13)	20.9 (17-25)
Duration of each stage in days mean (range)	3.6 (3-6)	3.9 (3-4)	3.4 (3-4)	10.6 (8-14)	

At 25° C, 25‰ salinity, development to first crab averaged 21 days (Table 1). Mean duration of each zoeal stage was 3 or 4 days while the megalopa lasted approximately 10 or 11 days. Mean sizes and ranges for five larvae at each stage are given in Table 2.

TABLE 2.—Size of *Hypoconcha subulosa* larvae stages, based on five larvae at each stage.

	Carapace length (mm)		Carapace width (mm)		Total length (mm)	
Stage	Mean	Range	Mean	Range	Mean	Range
Zoea I	1.30	1.20-1.37	0.72	0.66-0.74	2.39	2.21-2.50
Zoea II	1.49	1.40-1.55	0.81	0.73-0.88	2.51	2.33-2.70
Zoea III	1.62	1.51-1.70	0.90	0.85-0.93	2.90	2.81-2.92
Megalopa	1.60	1.54-1.64	1.20	1.11-1.24	—	—

Larval Description

Live *H. sabulosa* zoeae are strong, active swimmers which readily capture *Artemia salina* nauplii. At first sight they generally look like large, proportionally short and bulky pagurid zoeae. The zoeae have a generally reddish-brown color and are most noted by the distinctive line of chromatophores along the ventral and posterior carapace margin (Figure 1).

Figures of the larval stages show the most common arrangement of setal numbers observed. For the most part, the figures should be self-explanatory; the descriptive text is intended to note significant morphological features and outline setal numbers with observed variations.

Zoea I

Carapace (Figure 1A, a) without dorsal and lateral spines, rostrum directed anteriorly, ventrolateral carapace margin smooth. Carapace striated with crisscrossing fine ridges giving a textured "skinlike" appearance. At least one pair of transverse grooves evident, eyes sessile.

Abdomen (Figure 1A, a) without spines or distinct projections, somite six and telson fused, small pleopod buds may be present.

Telson (Figure 2A) triangular with distinct median notch; setation 7 + 7 with outer fixed spine, hairlike plumose seta, and five large plumose setae.

AN1 (Figure 3A) — Single segment; terminal setation of three aesthetascs and two simple setae; subterminal setation of two plumose setae.

AN2 (Figure 3E) — With 10 plumose setae on scale and 4 plumose setae on endopodite.

MN (Figure 4A, a) — With concave median surface and lateral serrate rim. Ventroposterior region with asymmetric group of teeth.

MAX1 (Figure 5A) — With two-segmented endopodite, distal segment with six setae, proximal segment with two setae; basal endite with three cuspidate and two plumodenticulate setae; coxal endite with four stout multidenticulate setae, three plumodenticulate setae, and one simple seta.

MAX2 (Figure 6A) — With indistinctly segmented endopodite, 2 or 3 setae; bilobed basal endite, distal lobe with 5 setae, proximal lobe with 5 setae, bilobed coxal endite, distal lobe with 5 setae, proximal lobe with 9 setae, scaphognathite with 17 or 18 marginal plumose setae. All setae plumose, plumodenticulate, or simple.

MXP1 (Figure 7A) — Exopodite with four plumose setae; endopodite five-segmented with numerous median margin setae and one lateral margin seta on distal segment.

MXP2 (Figure 7E) — Exopodite with four plumose setae; endopodite four-segmented with indicated pattern of median margin setae and one lateral margin seta on distal segment.

MXP3 — Limited to undeveloped bud.

P1 (Figure 7L) — Unsegmented biramous appendage with up to two plumose setae.

Zoea II

Carapace (Figure 1B, b) with same basic features as stage I but with two distinct pairs of transverse grooves; eyes stalked.

Abdominal somites (Figure 1B) with pleopod buds; somite six and telson partially fused.

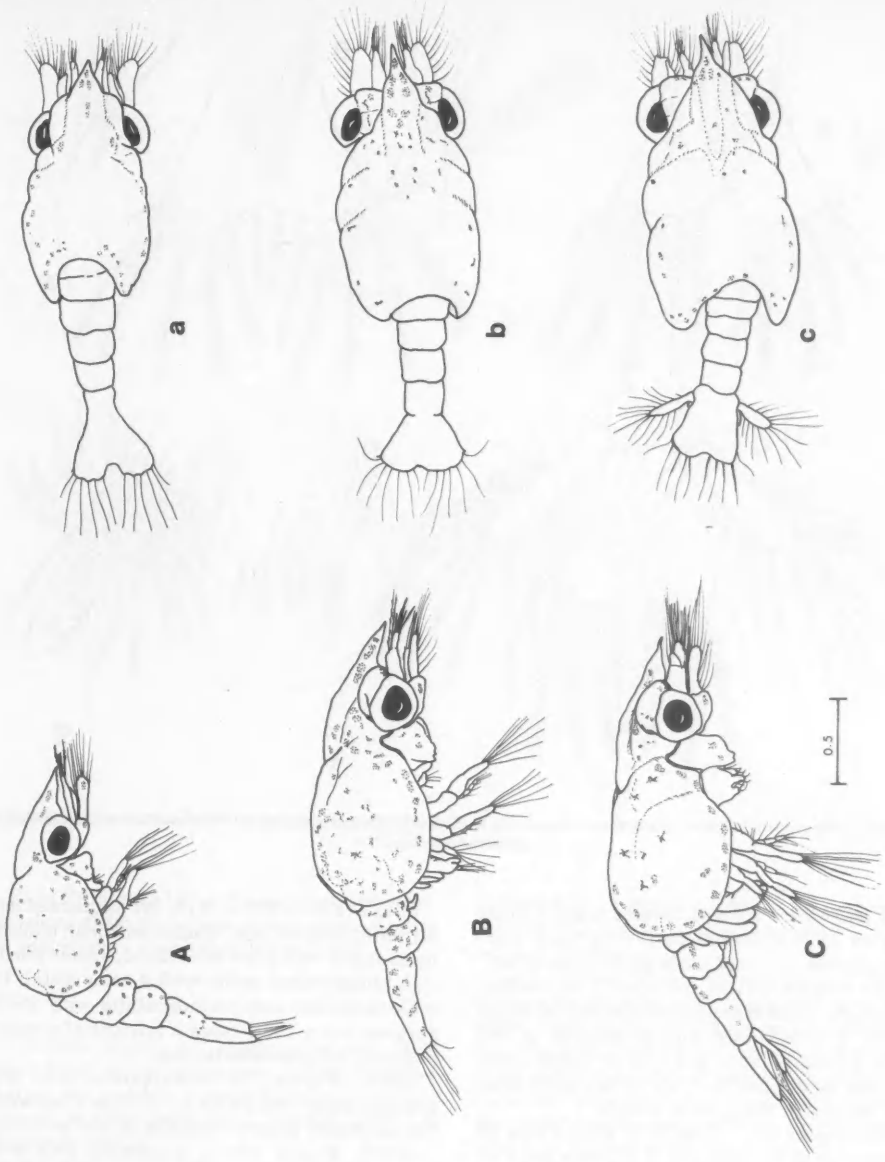

FIGURE 1.—*Hypoconcha sabulosa*: Lateral and dorsal view of zoeal stages I (A, a), II(B, b), and III (C, c).

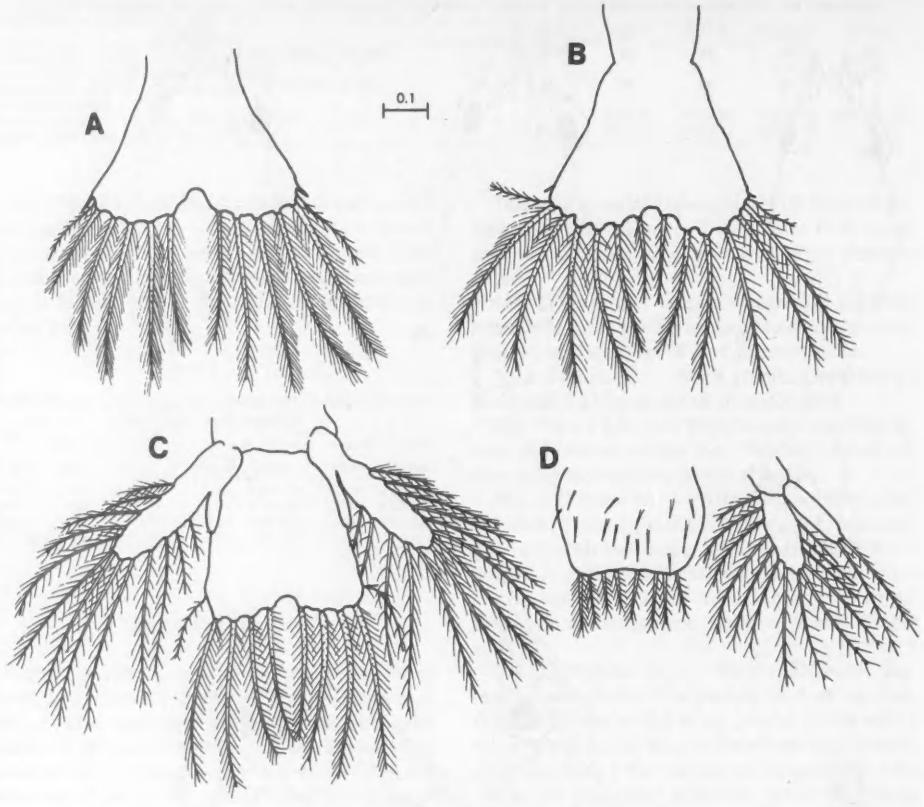

FIGURE 2.—*Hypoconcha sabulosa*: telson of zoeal stages I (A), II (B), and III (C), and megalopa (D). Only one disarticulated uropod is shown for megalopa.

Telson (Figure 2B) with reduced median notch; setation 8 + 8 with small outer fixed spine, hair-like plumose seta, and six large plumose setae.

AN1 (Figure 3B) — Indistinctly segmented; terminal setation of five aesthetascs and three fine simple processes; subterminal setation of two large plumose setae and two or three short plumose setae; additional one or two short setae may be present along basal margin.

AN2 (Figure 3F) — Similar to stage I with 19 plumose setae on scale and 3 plumose setae on endopodite.

MN — Similar to stage I; no palp.

MAXI (Figure 5B) — With major features as in stage I, basal endite (7 setae) and coxal endite (10 or 11 setae) with additional fine setae as indicated.

MAX2 (Figure 6B) — With two-segmented endopodite, 5 setae distal, 3 setae proximal; bilobed basal endite with 5 or 6 setae distal, 6 setae proximal; bilobed coxal endite with 4 setae distal, 11 setae proximal; and scaphognathite with 21-23 plumose setae. Setal types a mixture of simple, plumose, and plumodenticulate.

MXP1 (Figure 7B) — Exopodite with six plumose setae; endopodite as in stage I but with two additional plumose setae on lateral margin.

MXP2 (Figure 7F) — Exopodite with five plumose setae, endopodite as in stage I but with two additional plumose setae on lateral margin.

MXP3 (Figure 7I) — Exopodite with five plumose setae; endopodite indistinctly segmented with two to three plumose setae.

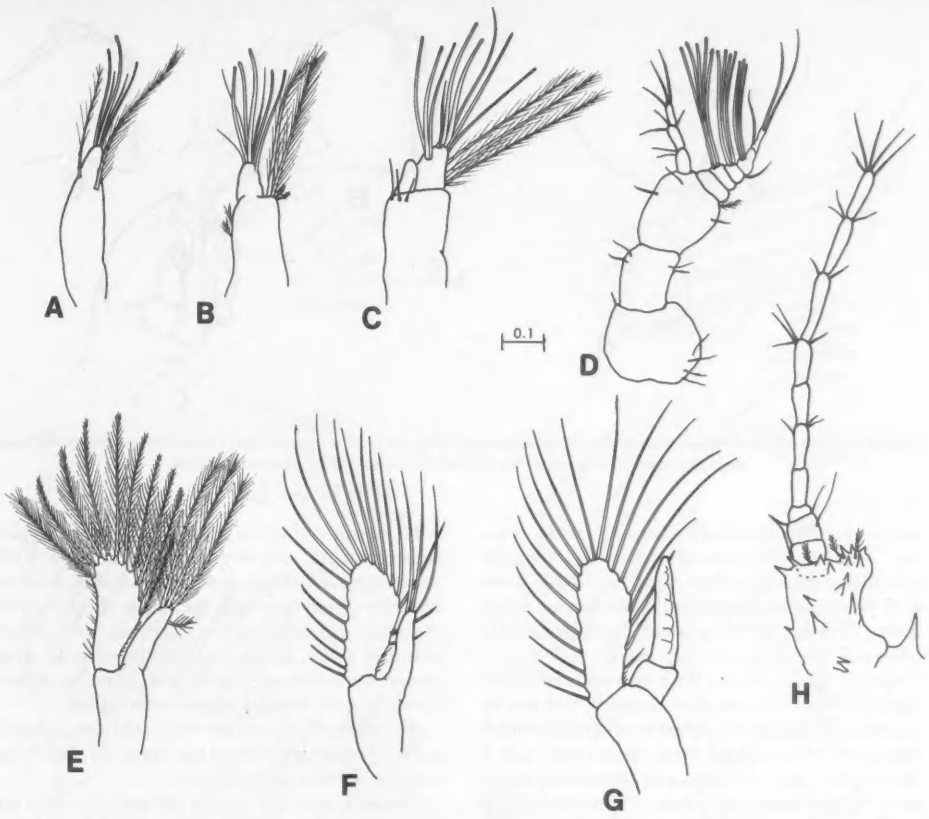

FIGURE 3:—*Hypoconcha sabulosa*: antennule of zoeal stages I (A), II (B), III (C), and megalopa (D); antenna of zoeal stages I(E), II (F), and II (G), and megalopa (H).

P1 to P5 (Figure 1B) — Conspicuous buds, first pereiopod distinctly biramous, four plumose setae on rudimentary exopodite (Figure 7M).

Zoea III

Carapace (Figure 1C, c) similar to stage II, a small blunt lateral spine near ventral carapace margin and posterior to second transverse groove present in some individuals; eyestalk with anterodorsal papilla.

Abdominal somites (Figure 1c) with elongated pleopod buds; sixth somite and telson distinctly segmented.

Telson (Figure 2C) normally 6 + 6 with very small outer spine, hairlike plumose seta, and 4 plumose setae; 2 zoeae 7 + 7 with 5 plumose setae, uropods with simple endopodite lobe and 13 or 14 setae on exopodite.

AN1 (Figure 3C) — Two-segmented; inner ramus a simple lobe; outer ramus with three terminal stout aesthetascs, three or four terminal fine processes (either simple setae or aesthetascs), three or four subterminal aesthetascs; basal segment with three stout plumose setae and three or four short plumose setae, also two short plumose setae (not figured) or proximal margin.

AN2 (Figure 3G) — With simple two-segmented endopodite and 18-21 plumose setae on scale.

MN (Figure 4B) — With simple palp.

MAX1 (Figure 5C) — With two-segmented endopodite, distal segment with two or three termi-

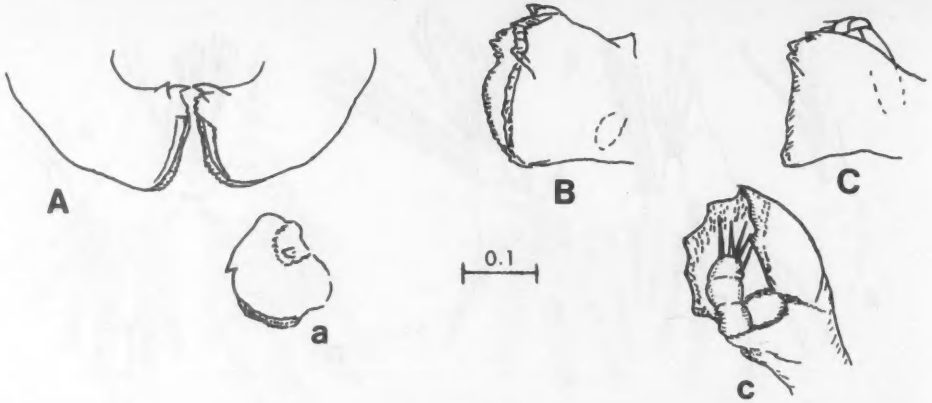

FIGURE 4.—*Hypoconcha sabulosa*: ventral view (A) and outline of biting survace (a) of stage zoeal I mandible: ventral view of zoeal stage III mandible (B); ventral view (C) and dorsal view (c) of megalopa mandible.

nal setae and two pairs of subterminal setae, proximal segment with two setae; basal endite with four or five stout cuspidate setae and five to seven finer plumose or plumodenticulate setae; coxal endite with six or seven stout multidenticulate setae and seven to nine finer setae.

MAX2 (Figure 6C) — With two-segmented endopodite, 5 setae on terminal segment, 3 or 4 setae on proximal segment; bilobed basal endite with 6 setae each lobe; bilobed coxal endite with 4 or 5 setae distal lobe, 14-17 setae in three rows proximal lobe (3 subterminal setae on opposite surface not figured); scaphognathite with 25-28 plumose setae.

MXP1 (Figure 7C) — Same as stage II but with one additional seta on endopodite lateral margin.

MXP2 (Figure 7G) — Exopodite with six or seven plumose setae; endopodite as in stage II but with additional seta on lateral margin.

MXP3 (Figure 7J) — Exopodite with six or seven plumose setae; endopodite with two distinct segments, four setae on terminal segment, one or two setae on proximal segment.

P1 to P5 (Figure 1C) — With pronounced extension beyond carapace; first pereiopod (Figure 7N) biramus, exopodite with six terminal setae; remaining pereiopods uniramus with segmentation evident and some simple setae or hairs.

Megalopa

Carapace (Figure 8A) dorsoventrally flattened with circular anterior margin and concave posterior margin; hepatic carapace margin with seven to nine distinct spines on each side, median anterior region depressed leading to short tapered rostrum; ventroposterior margins with short plumose setae; surface generally covered with numerous hairs, spinules, and plumose setae; eyestalk with distinct anterodorsal spine.

Abdominal segments with distinct lateral spines on segments two to six; dorsal surface with numerous hairs and spinules.

Telson (Figure 2D) nearly square, covered with hairs; anterior margin straight to slightly concave with 8 plumose setae; articulated uropods, endopodite with 2 plumose setae, exopodite with 13 or 14 plumose setae.

AN1 (Figure 3D) — With three basal segments; outer ramus with five segments, setation from tip to base, three simple setae, three or four aesthetascs, four aesthetascs, no setae; inner ramus with three segments with 2-3-2 setae.

AN2 (Figure 3H) — Basipodite with palp, numerous spines and three or four plumose setae; endopodite with 10 segments.

MN (Figure 4C, c) — With outer cutting edge and depressed center; palp three-segmented with five processes on distal segment.

MAX1 (Figure 5D) — With three-segmented endopodite, setation reduced to 6 setae as shown; basal endite with 7 cuspidate setae, 8 or 9 plumodenticulate setae, and 3 plumose setae on

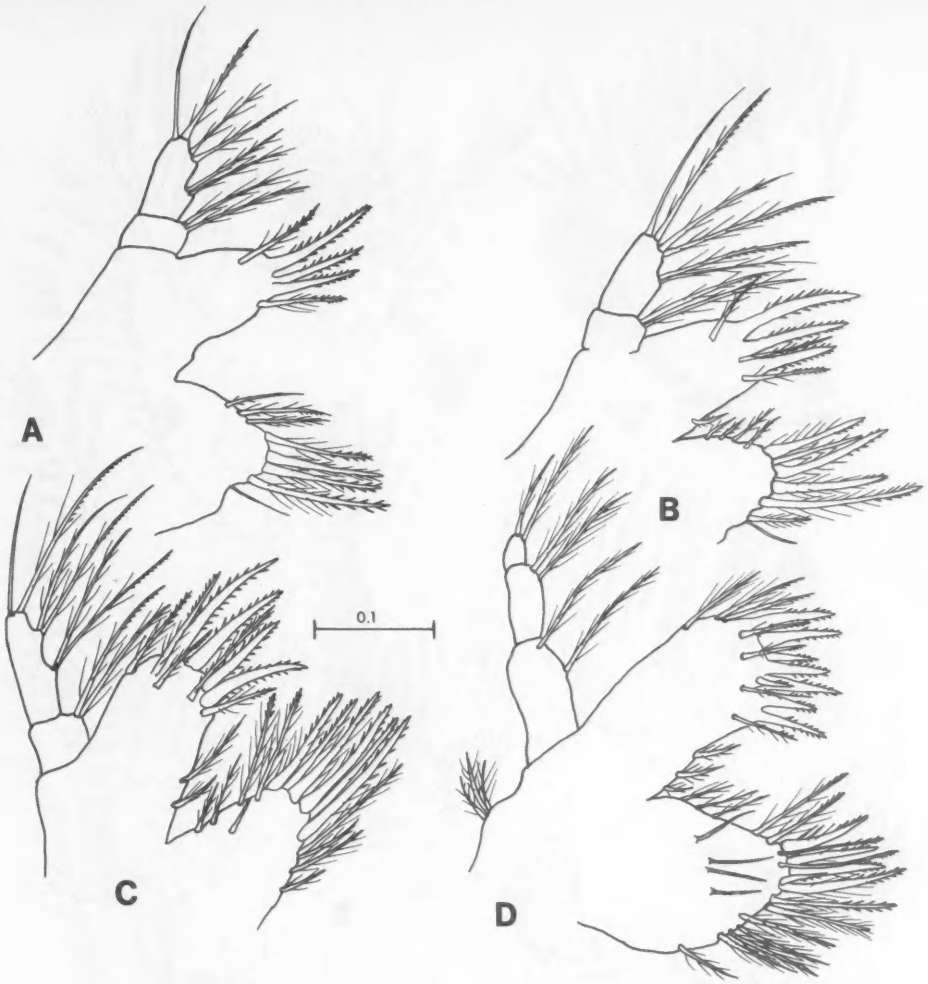

FIGURE 5.—*Hypoconcha sabulosa*: maxillule of zoeal stages I (A), II (B), and III (C), and megalopa (D).

proximal margin; coxal endite with 5 or 6 stout multidenticulate setae and 18-20 finer setae.

MAX2 (Figure 6D) — With two-segmented endopodite, 5 setae on terminal segment, 1 or 2 setae on proximal segment; bilobed basal endite with 9 setae distal lobe, 8-10 setae proximal lobe, bilobed coxal endite with 7-9 setae distal lobe, 20-22 setae proximal lobe; scaphognathite with 37-40 plumose setae.

MXP1 (Figure 7D) — Exopodite with 2 or 3 terminal and 2 or 3 subterminal plumose setae; endopodite indistinctly segmented with 8 setae; basipodite with 24-28 setae; coxapodite with about 15 setae.

MXP2 (Figure 7H) — Exopodite with 5-7 terminal and 2 subterminal plumose setae; endopodite five-segmented, 5 or 6 terminal setae and 8-10 setae subterminal.

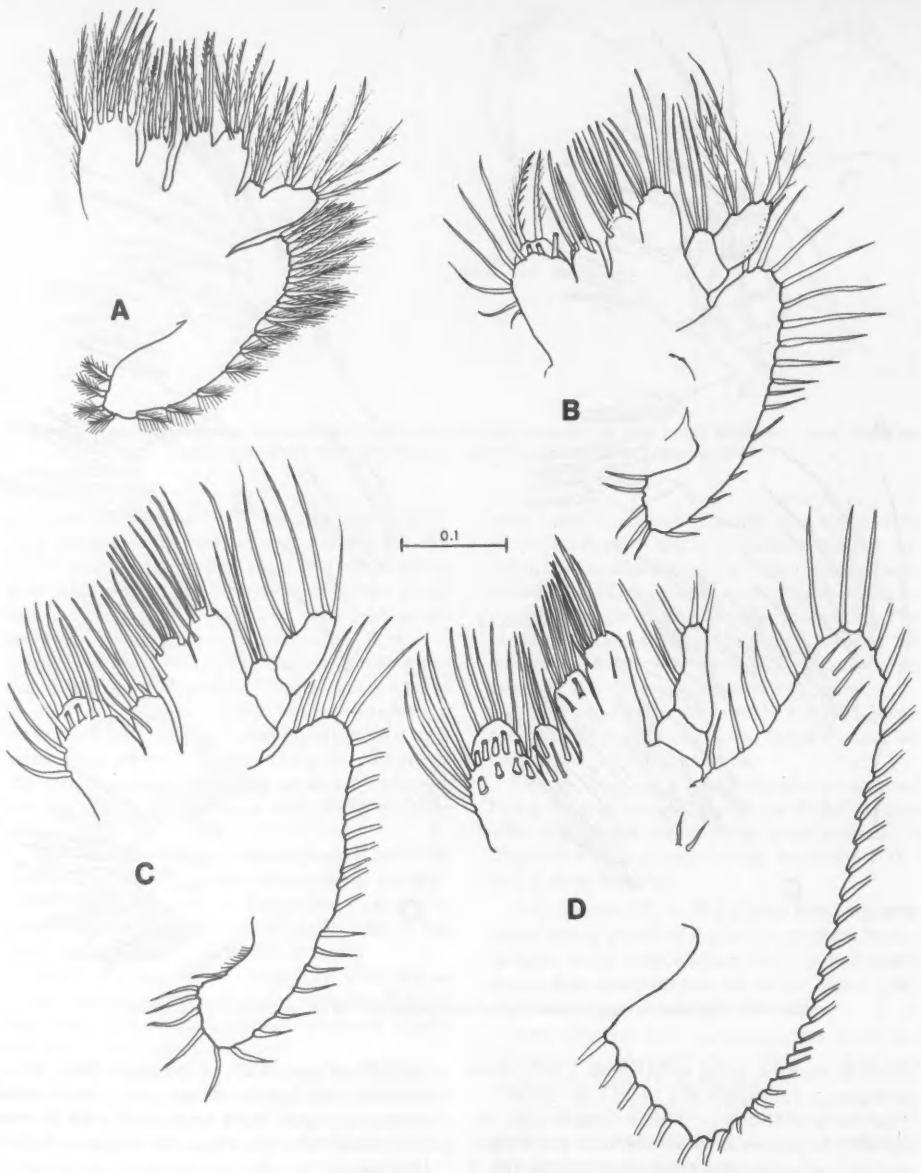

FIGURE 6.—*Hypoconcha sabulosa*: maxilla of zoeal stages I (A), II (B), and III (C), and megalopa (D). Setules have been omitted from B-D for graphic clarity.

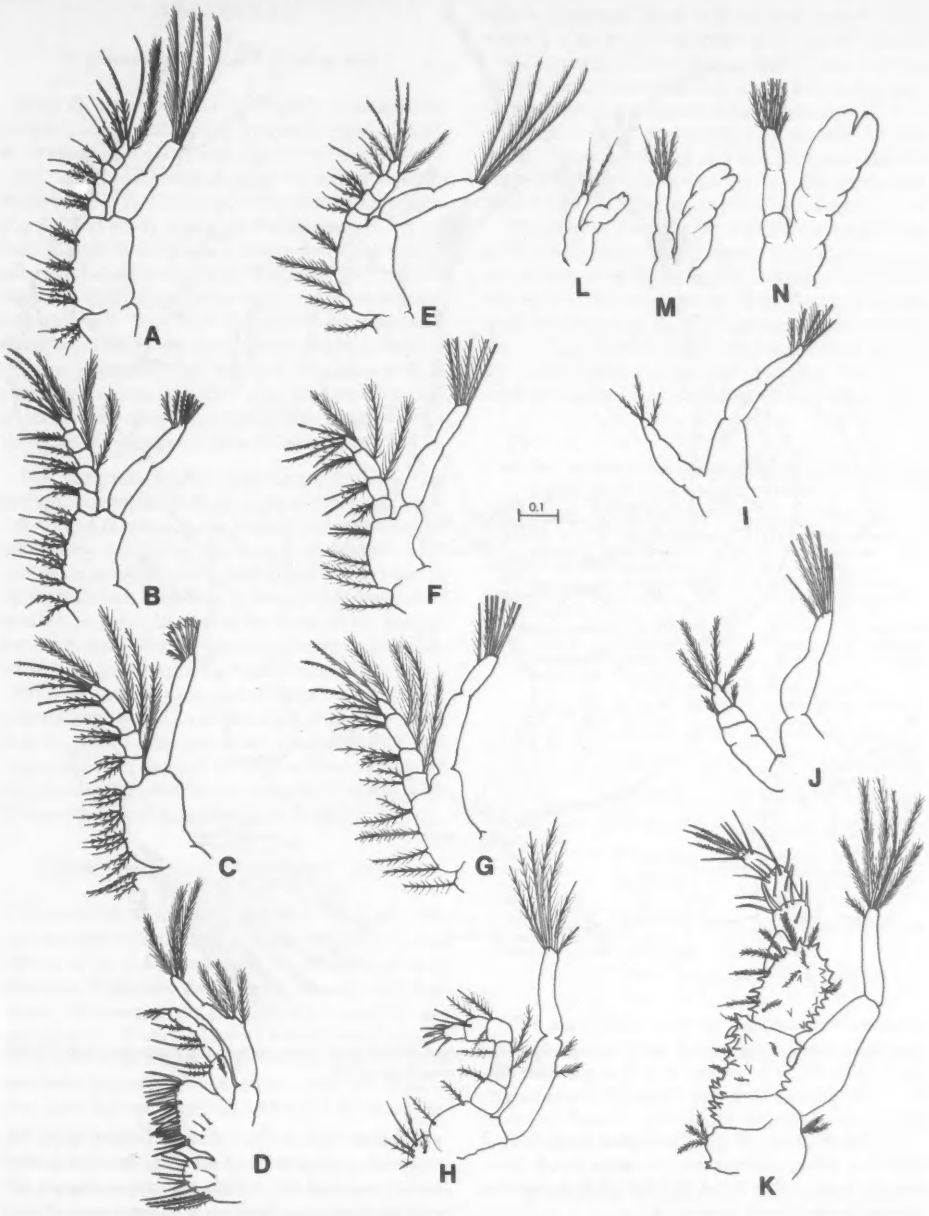

FIGURE 7.—*Hypoconcha sabulosa*: first maxilliped of zoeal stage I-megalopa (A-D); second maxilliped of zoeal stage I-megalopa (E-H); third maxilliped of zoeal stage II-megalopa (I-K); and first pereiopod of zoeal stage I-III (L-N).

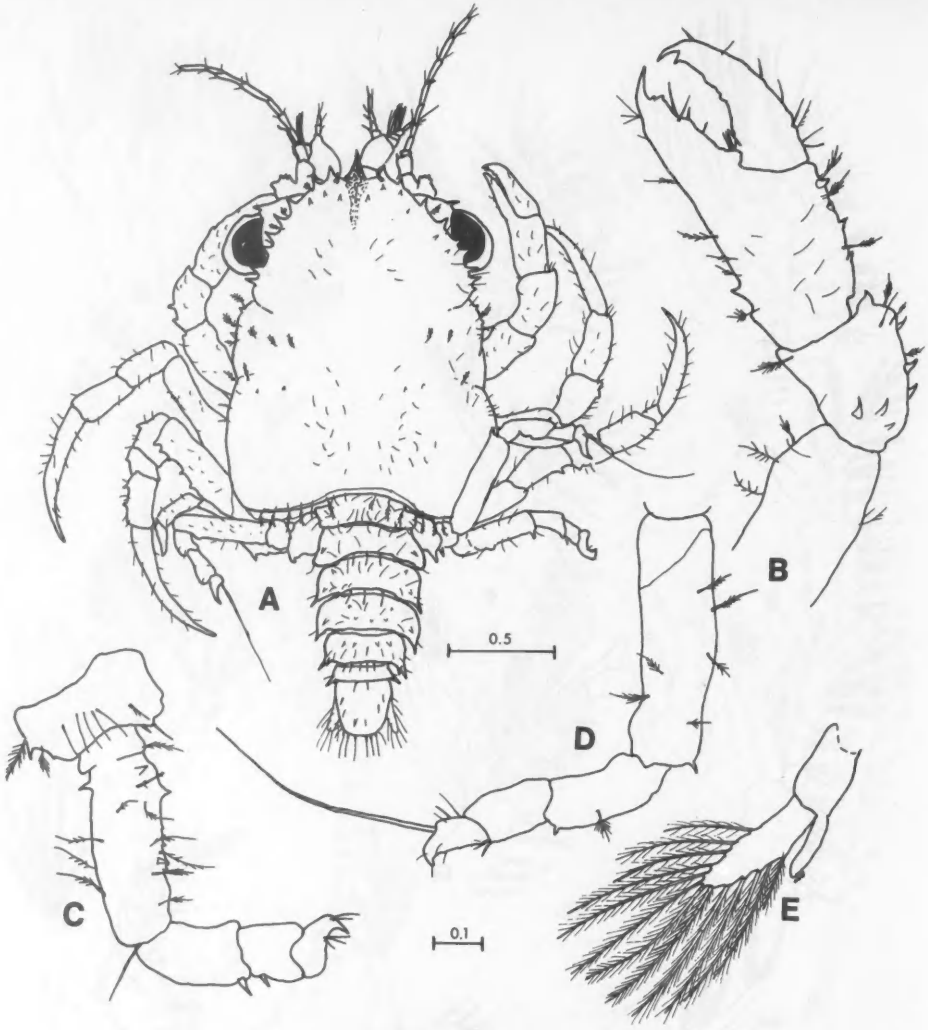

FIGURE 8.—*Hypoconcha sabulosa*: dorsal view of megalopa (A) and details of appendages; cheliped (B), fourth pereiopod (C), fifth pereiopod (D), and second pleopod (E).

MXP3 (Figure 7K) — Exopodite with 6 or 7 plumose setae; endopodite five-segmented, setation tip to base, 6 or 7, 6-8, 6, 10-12, 5-8, numerous spines on two lower segments.

P1 to P5 (Figure 8A-D) — Uniramous with numerous hairs and short plumose setae. First pereiopod (Figure 8B) with equal-sized claws; second and third pereiopod similar, dactylpods with simple tapered tip; fourth pereiopod (Figure 8C) shorter, dactylpod hooked; fifth pereiopod (Figure 8D) carried high and over carapace, dactylpod hooked with long stiff simple process.

DISCUSSION

Hypoconcha Species Distinction

Both *H. arcuata* and *H. sabulosa* have similar ranges and habitats along the southeastern United States coast (Hay and Shore 1918; Williams 1965) and adult morphology is quite similar (Rathbun 1937; Williams 1965). The source of larvae for this study was a small (carapace 17 × 17 mm) female with characteristics dorsal carapace, color, and marginal spines (Williams 1965). However, the ventral carapace ridges were weakly developed and the three characteristic tubercles (Rathbun 1937) were not evident (one small tubercle was present). This may be characteristic of young specimens or it may indicate hybridization of the two species. The distinction of species for these two forms should perhaps be reinvestigated.

Not surprisingly, the differences between the larval morphology of *H. arcuata* given by Kircher (1970) and *H. sabulosa* are slight. The differences we observed overlap the ranges of variation reported for setation or represent fine points open to interpretation. Based on present published information, a reliable means to distinguish corresponding zoeal stages between the two species is absent. *Hypochoncha sabulosa* megalopae have spines on the eyestalk and abdominal segments, features not noted for *H. arcuata*. However, these may be points of omission by Kircher (1970) and represent only tentative differences. A detailed direct comparison of larvae is needed to determine if these species can be identified during ontogeny.

Characteristics of Dromiidae Larvae

Knowledge of dromiid larvae is limited to five genera within the family Dromiidae (Table 3). The larvae of *H. sabulosa* demonstrate most general features of dromiid larval development; some features, however, such as carapace armature are surprisingly diverse. Larval development ranges from six zoeal stages in *Dromidia antillensis* to two zoeal stages in *Conchoecetes artifiosus*. Four of ten documented species have abbreviated development (Table 3).

The dromiid zoeal carapace is elongated with a large, anteriorly directed rostrum, transverse grooves, and, in most cases, a textured surface of fine ridges. The carapace may lack armature (*Hypoconcha, Conchoecetes*), have posterolateral spines (*Dromia*), have supraorbital spines (*Dromidia*), or have a dorsal spine and lateral "wings" (*Petalomera*). Carapace margins are either smooth or denticulate. All zoeae are richly pigmented with a general orange-red color.

The antennal morphology is unique to the group. The endopodite has 3 or 4 plumose setae in stage I larvae. The exopodite is a flat scale and after stage I has setae on its outer margin.

The mandibular palp generally does not develop until the terminal zoeal stage while the maxilla endopodite is well developed and often distinctly segmented. The endopodites of the first and second maxillipeds are five- and four-segmented respectively. The third maxilliped is usually biramous and rudimentary in stage I but well developed with a basally situated endopodite by stage II.

TABLE 3.—Principal studies on the postembryonic development in taxa of the family Dromiidae.

Taxon	Author	Material
Dromiidae	Gurney (1924)	Plankton sample with
	Gurney (1942)	unknown parents
Conchoecetes artifiosus	Sankolli and Shenoy (1968)	Laboratory—all stages
Cryptodromia octodentata	Hale (1925)	Abbreviated development
Dromia personata	Cano[1](1893)	Plankton—I, IV, megalopa
	Williamson[1] (1915)	Plankton—I, IV, megalopa
	Lebour[1] (1934)	Plankton—I,II,IV, megalopa
	Pike and Williamson[2](1960b)	Plankton—I,II,III
	Rice et al. (1970)	Laboratory—all stages
Dromidia antillensis	Rice and Provenzano (1966)	Laboratory—all stages
Dromidia australis	Hale (1927)	Abbreviated development
Epipedodromia thomsoni	Hale (1925)	Abbreviated development
Hypoconcha arcuata	Kircher (1970)	Laboratory—all stages
Hypoconcha sabulosa	Present paper	Laboratory—all stages
Petalomera lateralis	Montgomery (1922) Hale (1925)	Abbreviated development
Petalomera wilsoni	Wear (1970)	Plankton—I, II
	Wear (1977)	Plankton—magalopa

[1]Described as *Dromia vulgaris*,
[2]Described as *Dromia personatus*.

The pereiopods may be uniramous (*Conchoecetes, Petalomera*) or biramous (*Dromidia*). Only the first pereiopod is biramous in *Dromidia* and *Hypoconcha*. Uropods are well developed in late zoeae of *Dromia, Dromidia,* and *Hypoconcha* but are reduced in *Conchoectes* and *Petalomera*.

Systematic Position of the Dromiidae

The classification and phylogeny of the Dromiidae and other decapod groups rests princi-

pally on three lines of evidence: comparative morphology, fossil records, and larval development (Stevcic 1971). Based primarily on comparative morphology of adult crabs and sparse fossil records, the family Dromiidae has usually been considered primative but true brachyurans (Balss and Grunner 1961; Burkenroad 1963; Glaessner 1969; Hartnoll 1975; Warner 1977).

In contrast to these findings, the larval development of dromiids is, in many aspects, typically anomuran. Gurney (1924) found all larvae of *Dromia* to be "definitely Anomuran." Brachyuran and anomuran larvae have since been well characterized in several comprehensive studies (Gurney 1942; Pike and Williamson 1960a; Williamson 1974); the findings of Gurney (1924) have been consistently substantiated. The megalopa is not so easily characterized and appears to more closely resemble its parents than both postlarval anomurans and nondromiid brachyurans (Wear 1977). A detailed account of the classification of the Brachyura and a proposed new system has recently been published by Guinot (1978).

The Brachyura are characterized not only by the advanced organizational level of adults but also by a consistant larval form. The evolutionary path should include "brachyurization" to both a crab body (Stevcic 1971) and a "brachygnath zoea" (Williamson 1974). A key to better understanding the dromiids is to find larval types which appear to lead toward a brachygnath form. If, like the Dromiidae, the Dynomenidae and Homolodromidae are found to have larvae showing no tendency to develop brachygnath features, the Dromiacea (Guinot 1978) may have progressed toward a crablike form independent of lines leading toward the true brachyurans.

The combination of adult and larval characteristics exhibited by the Dromiidae has not been satisfactorily explained. In view of obvious contradictions and the relative importance of adult morphology in decapod classification, removal of the Dromiidae from the Brachyura based solely on known larval features (Gurney 1924, 1942; Kircher 1970; Williamson 1974) is not warranted. Placement of the Dromiidae within the Brachyura, is by no means "of little doubt" as claimed by Warner (1977) but represents more a matter of convenience (Guinot 1978); their position is tenuous at best. Hopefully additional material (larval, morphological, or fossil) will lead to a comprehensive account of the Dromiidae and related families.

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BLACK ROCKFISH, *SEBASTES MELANOPS*: CHANGES IN PHYSICAL, CHEMICAL, AND SENSORY PROPERTIES WHEN HELD IN ICE AND IN CARBON DIOXIDE MODIFIED REFRIGERATED SEAWATER

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ABSTRACT

The purpose of this study was to determine changes in various properties of fillets, minced flesh, and washed minced flesh from black rockfish, *Sebastes melanops*, as affected by time of holding in ice or carbon dioxide modified refrigerated seawater and frozen storage at -18° C. Fish were held up to 14 days in the holding mediums and removed periodically and analyzed for changes in physical, chemical, and sensory properties. The yield of fillets calculated from the initial whole weight was unaffected by time of holding in either system. Subjective observations made during the holding periods indicated that fillets of good quality could be prepared from rockfish held for 10 days in either system. These observations were confirmed in a later series by sensory evaluation of cooked portions from the frozen blocks of fillets prepared at intervals during an 11-day holding period. The chemical analyses for trimethylamine, total volatile acid, and total volatile base were of no use to measure spoilage. Washing the minced flesh resulted in a reduction of solids, trimethylamine oxide, and salt and a reduction in yield when expressed on a salt-free constant, 18% solids basis. The extractable protein nitrogen of minced flesh decreased with time of frozen storage at -18° C and was strongly influenced by the length of holding period for the fresh whole fish.

Several papers have been published on the fresh or frozen characteristics of fillets or minced flesh from rockfishes. Different species of rockfishes gave products having different fresh acceptability and frozen storage life (Miyauchi and Stansby 1952). Stansby and Dassow (1949) found that the frozen storage quality of fillets from yellowtail rockfish, *Sebastes flavidus*, could be improved by removing part of the dark flesh along the lateral line. Barnett et al. (1971) compared yellowtail rockfish held in refrigerated seawater (RSW) and RSW modified with the addition of CO_2 (MRSW). The fresh storage life was extended 1 wk in MRSW over RSW. Teeny and Miyauchi (1972) increased the frozen life of minced flesh of yellowtail rockfish and silvergray rockfish, *S. brevispinis*, by using various additives. Additional improvements in storage life were obtained by washing the minced muscle of black, silvergray, and yellowtail rockfishes (Miyauchi et al. 1975.)

The objectives of this study were generally to characterize and compare the changes that occur in black rockfish with time of holding in ice and in MRSW, to determine sensory properties of fillets as affected by fresh holding time, and to determine the changes in amine content and extractable protein nitrogen with time of frozen storage of washed and unwashed minced flesh.

EXPERIMENTAL PROCEDURES

Sampling

Two groups of fish were used in this study. Lot 1 was used to determine physical and chemical properties and Lot 2 was used for formal sensory evaluation. The fish were caught over a 2-h period with hook and line, with or without bait. These fish are found locally on exposed, highly sloped rocky shores with strong currents where trawling gear cannot be used. A sporadic local fishery has employed the same fishing technique. Lot 1 fish (154 fish, 265 kg, 0.2 kg SD) were captured 2 July 1977 at the Triplets, 20 mi northwest of Kodiak, Alaska, and delivered to the laboratory about 2 h later. The fish were individually tagged and weighed before placing in the previously described ice and MRSW holding systems (Bullard and Collins 1978). The raw fish handling and sample preparation were similar to that previously reported for walleye pollock (Reppond et al. 1979), and are briefly described here. Fish were sampled according to weight classes to give an average of

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1.8 kg/fish for an 11-fish sample at holding periods of 0, 4, 6, 8, 10, 12, and 14 days. When removed from the holding systems, the fish were washed briefly to remove slime or ice, drained on a rack for 5 min, and individually weighed. The fish were filleted by hand and the fillets were rinsed briefly, drained on an inclined screen for 5 min, and weighed. Notes were made on the appearance of the round fish and the condition of the gills, viscera, and fillets. The fillets were ground using the coarse blade of an Oster[2] food grinder, and a portion was washed with cold water (1 part flesh: 2 parts water) for 15 min on a reciprocating shaker. The flesh was drained for 30 min on an inclined 16-mesh plastic screen then weighed. Composite portions of both washed and unwashed meats were frozen at -34° C for chemical tests. Other portions were sealed in polylaminated pouches and stored at -18° C for 2, 4, 6, and 9 mo.

Sensory

Lot 2 fish (184 fish, 258 kg) were used for formal sensory testing and were caught in the same location 1 mo later, on 26 August. These fish were held in ice and in MRSW in the same manner as Lot 1 and at 0, 3, 6, 8, and 11 days were filleted. The fillets were packed into blocks and held at -34° C for sensory evaluation several months later. The blocks were sawed into portions measuring 80 × 50 × 12 mm and thawed at room temperature. The control sample and samples from fish held in ice were salted by immersion in a 5% solution for 1.5 min to minimize differences in salt content with samples from fish held in MRSW. The portions were cooked in individual sealed aluminum pans at 232° C for 20 min in a commercial oven. Because of the difficulty in equalizing the salt content, samples from the two holding systems were not directly compared. The results of the sensory test were evaluated by analysis of variance. If analysis of variance indicated a change had occurred with time of holding, the Student-Newman-Keuls test was used to determine which samples were different.

Analyses

The frozen samples for chemical tests (Lot 1) were tempered overnight in a refrigerator at 3° C and ground twice using the fine blade of an Oster food grinder. Analyses were carried out for total nitrogen, total solids, chloride (Horwitz 1975: 15, 309, 310), total volatile acid (TVA, Friedemann and Brook 1938), total volatile base (TVB, Stansby et al. 1944), and extractable protein nitrogen (EPN, Dyer et al. 1950). Analyses for trimethylamine oxide (TMAO, Bystedt et al. 1959), nonprotein nitrogen (NPN, Nikkilä and Linko 1954), and trimethylamine (TMA, Tozawa et al. 1971) were carried out on a 5% trichloroacetic acid extract. An aliquot of the extract was neutralized and analyzed for dimethylamine (DMA) by Dowden's method (1938) modified by increasing the time of extraction to 15 min on a mechanical shaker.

RESULTS AND DISCUSSION

Physical Appearance and Yield

At each period of sampling, informal subjective observations were made on the whole fish and their raw fillets. We noted differences in gills, fins, and slime between the two holding systems. In ice, the gills were bright red to day 6 but discolored quickly in MRSW. Cloudiness of the eyes started at day 8 in ice but the eyes were white in a day or two in MRSW. The beginning of off-odors in the fillets, softening of flesh, and gut decompostion was observed in both holding systems at 10 days and worsened thereafter. At day 14, the odor of the fillets was objectionable and mincing intensified the odor. The quality of fillets from the fish held in MRSW were generally judged better than from fish held in ice for the same time. As noted later in this paper, neither formal sensory nor chemical tests detected the changes observed on the 10th day of holding in ice or MRSW. Chemical tests could not confirm the poor raw quality at 12 and 14 days which was so obvious that we would not serve these fillets to a taste panel. Consequently, we concluded that experienced observers could subjectively judge the various stages of raw quality, namely: good quality (0-8 days), onset of spoilage (10 days), and unacceptable quality (12 days).

Whole fish gained weight with time of holding in either system (Table 1). Fish held for 14 days in ice gained half as much weight as those held in MRSW, about 3% and 6%, respectively. The yield of fillets increased slightly with time of holding in ice but was constant with time of holding in MRSW. The average yield of fillets was slightly

[2]Reference to trade names here does not imply endorsement by the National Marine Fisheries Service, NOAA.

higher from fish held in ice than from fish held in MRSW, 31.7% and 30.5%, respectively. When yield data are converted to a salt-free, 18% solids basis however, equal yields of fillets were obtained in both systems (34%). The solids content of the fillets decreased slightly in ice but increased in MRSW because of the increase in salt content (Table 1). The absorption of salt from the MRSW system is not a problem because rockfish have thick flesh and skin.

TABLE 1.—Initial round weight and change in yield, salt, and total solids content of fillets and washed ground flesh from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Round wt[1] (kg)	Gain in wt (%)	Fillets			Washed ground flesh		
			Yield (%)	Salt (%)	Solids (%)	Yield[2] (%)	Salt (%)	Solids (%)
			Ice					
0	18.35	0.00	30.7	0.03	20.2	40.5	0.05	15.0
4	19.09	1.15	31.0	0.07	19.2	36.5	0.04	14.8
6	18.88	1.51	31.5	0.09	19.5	38.5	0.06	13.8
8	19.48	2.08	31.8	0.10	19.4	38.9	0.08	13.5
10	19.51	2.15	31.2	0.10	19.3	38.5	0.06	13.3
12	19.66	2.74	32.1	0.09	19.1	39.3	0.04	13.1
14	21.49	2.75	32.7	0.08	19.1	40.0	0.07	13.0
			Modified refrigerated seawater					
0	18.35	0.00	30.7	0.03	20.2	40.5	0.05	15.0
4	19.90	2.56	30.4	0.20	20.2	36.8	0.08	14.2
6	19.35	3.89	30.6	0.28	20.6	34.7	0.11	15.0
8	19.26	4.25	30.0	0.36	20.4	34.0	0.14	14.8
10	18.93	4.40	30.4	0.48	20.7	34.2	0.20	15.3
12	19.48	6.27	30.8	0.57	20.9	33.5	0.22	16.1
14	18.81	5.65	30.6	0.76	20.9	32.9	0.27	16.8

[1]Total round weight of fish that composed the sample.
[2]Yield of washed ground flesh if no portion had been reserved for analysis of fillets.

TABLE 2.—Change in mean sensory analysis scores ± standard deviations for baked portions of blocks of fillets from black rockfish (Lot 2) with time of holding in ice and in modified refrigerated seawater (MRSW). Panel had 12 judges. Flavor and texture scores were on the following scale: 5-Very good, 4-Good, 3-Fair, 2-Borderline, and 1-Poor. Preference scores were on a 9-point scale: 9-Like extremely, 8-Like very much, 7-Like moderately, 6-Like slightly, 5-Neither like nor dislike, 4-Dislike slightly, 3-Dislike moderately, 2-Dislike very much, and 1-Dislike extremely.

Time of holding (days)	Flavor		Texture		Preference	
	Ice	MRSW	Ice	MRSW	Ice	MRSW
0	3.5±0.7		4.1±0.6		6.3±1.4	
3	3.1±0.4	3.8±0.6	3.9±0.7	4.1±0.3	5.8±0.7	6.4±1.3
6	3.4±0.7	3.6±0.5	4.1±0.5	4.0±0.4	6.3±1.2	6.3±0.9
8	3.6±0.6	2.9±0.8	4.3±0.5	3.8±0.6	6.5±1.0	5.2±1.3
11	3.5±0.8	3.1±0.5	4.0±0.5	3.8±0.6	6.4±1.3	5.4±1.2

Sensory Evaluation

No significant ($P<0.05$) change in flavor, texture, or preference was noted between the zero time control and any sample from either holding system (Table 2). No significant differences in sensory scores occurred among the ice-held samples but the differences in flavor and preference scores between samples held 3 days and 8 days in MRSW were significant. However, these differences were probably circumstantial since neither the 3- nor 8-day MRSW sample differed from any of the other samples from that holding system.

The bland flavor of rockfish flesh was reflected in the preference scores which ranged from "like slightly" to "neither like nor dislike." The sensory data indicate that when held in ice or in MRSW this species of rockfish will maintain its acceptability during commercial holding periods of at least 8 to 10 days.

Chemical Analyses

The protein content of fillets (Table 3) was unaffected by time of holding but was slightly lower from fish held in ice than in MRSW. The nonprotein nitrogen content decreased slightly with time of holding in both holding systems.

Several chemical tests were performed to measure spoilage. TVA values increased from 0.07 at 8 days in ice to 0.10 meq/100 g at 10 days which may indicate a change in quality at 10 days. No change was noted in fillets from the MRSW system. TVB values were constant and low (about 4 mg N/100 g). As with walleye pollock, TVB data were not useful to indicate spoilage. TMA values increased

TABLE 3.—Change in analytical values of fillets from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Ice						Modified refrigerated seawater					
	Protein[1] (%)	NPN (%)	TVA (meq H^+/100g)	TVB (mgN/ 100 g)	TMA (mg N/ 100 g)	DMA (mg N/ 100 g)	Protein[1] (%)	NPN (%)	TVA (meq H+/100 g)	TVB (mg N/ 100 g	TMA (mg N/ 100 g)	DMA (mg N/ 100 g)
0	18.3	0.34	0.06	3.9	0.20	0.20	18.3	0.34	0.06	3.9	0.20	0.20
4	18.5	0.33	0.06	3.6	0.41	0.30	18.8	0.32	0.06	3.3	0.37	0.23
6	18.8	0.31	0.06	—	0.41	0.24	19.0	0.31	0.07	—	0.43	0.23
8	18.3	0.31	0.07	—	0.49	0.27	19.0	0.30	0.06	2.8	0.49	0.29
10	18.4	0.31	0.10	—	0.59	0.29	19.2	0.30	0.06	—	0.56	0.18
12	18.2	0.30	0.11	—	0.62	0.30	19.1	0.30	0.07	2.9	0.67	0.37
14	18.4	0.30	0.10	3.9	0.82	0.24	19.0	0.27	0.08	—	0.69	0.29

[1]6.25 N.

in an equal, gradual and linear manner with time of holding in both systems. DMA values did not change with time of holding or system (0.3 mg DMA-N/100 g).

Effects of Washing Minced Flesh

Washing the minced flesh of black rockfish resulted in a reduction in salt and solids content (Table 1), in slightly lower EPN values (Table 4), and a big drop in TMAO content (Table 5). Washing increased the apparent yield of minced fillets from 32 to 38% (ice) and from 32 to 33% (MRSW). When yield data of fillets and minced, washed flesh are placed on a comparable basis by converting to a salt-free, constant 18% solids basis however, the washing procedure reduced the yield in both systems from 34 to 28%.

Frozen Storage

A number of research papers have been published on the general subject of toughness of fish flesh and the relationship (or not) of free fatty acids, formaldehyde, and EPN (Mills 1975). The tough texture that develops in frozen fish is always accompanied by a decrease in EPN (Castell et al. 1973) but texture and EPN are not necessarily equated. It is generally accepted that reduced EPN occurs with increased fatty acid content and formaldehyde content (sometimes indirectly measured as DMA). The extractable protein nitrogen (Table 4) of minced flesh from ice-held fish decreased slightly at 2 and 4 mo of frozen storage, decreased to about 50% at 6 mo, and decreased to about 35% at 9 mo. The same general trend was observed with MRSW-held fish except EPN values

TABLE 4.—Change in extractable protein nitrogen content (percent) of minced flesh (unwashed and washed) from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Ice					Modified refrigerated seawater				
	Months of frozen storage at -18° C					Months of frozen storage at -18° C				
	0	2	4	6	9	0	2	4	6	9
	Minced flesh					Minced flesh				
0	85	87	70	60	32	85	87	70	60	32
4	83	83	68	64	42	85	—	73	70	31
6	80	72	78	46	42	80	63	64	59	24
8	87	74	73	54	37	86	53	73	42	26
10	78	70	77	53	34	78	56	65	38	30
12	82	69	72	33	35	73	56	60	49	24
14	86	73	64	48	27	74	48	39	26	22
	Washed minced flesh					Washed minced flesh				
0	90	79	63	56	30	90	79	63	56	30
4	77	79	75	59	33	78	61	58	57	32
6	83	76	74	62	29	75	65	63	42	28
8	81	69	70	38	34	79	71	60	28	26
10	77	75	62	49	34	83	45	54	27	19
12	83	77	66	31	26	67	44	44	23	21
14	74	70	63	42	26	68	40	47	23	15

TABLE 5.—Change in trimethylamine oxide content (milligrams TMAO-N/100 g) of minced flesh (unwashed and washed) from black rockfish (Lot 1) with time of holding in ice and in modified refrigerated seawater.

Time of holding (days)	Ice					Modified refrigerated seawater				
	Months of frozen storage at -18° C					Months of frozen storage at -18° C				
	0	2	4	6	9	0	2	4	6	9
	Minced flesh					Minced flesh				
0	136	100	68	69	74	136	100	68	69	74
4	130	97	56	66	70	145	98	70	67	69
6	128	96	66	65	66	140	93	68	63	66
8	129	92	66	60	64	127	86	63	66	62
10	125	86	64	60	66	126	85	63	58	62
12	143	84	64	60	66	121	83	62	58	59
14	143	86	63	63	61	120	83	59	61	56
	Washed minced flesh					Washed minced flesh				
0	36	—	37	36	39	36	—	37	36	39
4	30	—	29	28	29	27	—	30	25	27
6	28	—	26	28	26	24	—	25	23	23
8	25	—	26	25	26	25	—	26	24	26
10	26	—	27	24	26	24	—	25	23	24
12	24	—	26	26	24	22	—	25	26	23
14	22	—	25	25	23	20	—	23	22	22

were slightly lower. Although EPN did not change significantly with time of fresh holding in ice and only slightly in MRSW, the effect of the length of time of fresh holding on EPN became apparent in samples held at -18° C for 6 to 9 mo. If EPN is related to the texture of black rockfish, the data in Table 4 suggest that 6 mo of frozen storage at -18° C was too long for minced flesh at any level of fresh quality and that various periods of frozen storage would give acceptable texture depending on the level of fresh quality when frozen.

The TMAO content of the unwashed minced flesh was unaffected by time of holding in ice but decreased slightly in MRSW (Table 5). Although not expected to change with the frozen storage of this non-gadoid fish, amine data were obtained since no data on TMA and DMA and only one value for TMAO (93 mg N/100 g, Dyer 1952) have been reported in the literature for *S. melanops*. There was a strong reduction in TMAO content of the unwashed minced flesh with time of frozen storage to 4 mo with little change thereafter. TMA and DMA values were not affected by frozen storage (data not included in tables). Consequently, the substantial reduction in EPN was not caused by formaldehyde. We cannot explain either the observed loss of TMAO without a concomitant increase in either TMA or DMA content or the lack of change in TMAO content with time of frozen storage of the unwashed minced flesh.

SUMMARY

Black rockfish was held in the round in ice or MRSW to 14 days. The yield of fillets was not affected by time of holding but fish held in ice gave slightly higher yields than fish held in MRSW, 32 and 31%, respectively. The usual chemical spoilage tests (TMA, TVA, TVB) were of little or no use as indicators of spoilage. Observations of the beginning of off-odors, softness of flesh, and decomposition of viscera at 10 days were not confirmed by sensory evaluation of the cooked portions. For this species, early changes in quality were best judged subjectively on the raw, whole fish and fillets. Formal sensory evaluation was less sensitive than informal evaluation to change in quality, and chemical spoilage tests were not sensitive to obviously advanced spoilage. Washing the minced flesh resulted in a reduction in salt, solids, and TMAO content. The yield increased with washing because of increased water content but when calculated on a salt-free, constant 18% solids basis, the yield decreased in both systems to 28% when minced and washed. The EPN values of minced flesh from ice-held fish decreased during frozen storage at -18° C from about 80 to 35% after 9 mo and MRSW-held fish gave similar but slightly lower EPN values. The degree of fresh quality strongly influenced EPN values during frozen storage indicating that the time of holding in ice or MRSW should be considerably less than 10 days to maintain good quality for any reasonable period of frozen storage.

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BEHAVIOR AND ECOLOGY OF THE DUSKY DOLPHIN, *LAGENORHYNCHUS OBSCURUS*, IN THE SOUTH ATLANTIC

BERND WÜRSIG AND MELANY WÜRSIG[1]

ABSTRACT

Dusky dolphins were present in Golfo San José, Chubut, Argentina, during most of the year, with a seasonal low in abundance during winter and a high in summer. The presence of the prey species southern anchovy, *Engraulis anchoita*, appeared to affect seasonal movements.

Surface feeding was highly visible and birds also fed on fish schools which dolphins herded to the water surface. Surface feeding occurred mainly in spring and summer in the study area, and in late summer and fall in more oceanic waters near the mouth of the bay. This surface feeding pattern corresponded with the presence of southern anchovy.

Dolphins moved in small groups of about 15 individuals while resting in early morning and while looking for food in late morning. Group sizes increased during surface feeding as groups joined existing feeding activity. Because surface feeding occurred mainly around noon and early afternoon, group sizes increased at those times. Dives were longer before and during feeding, and shorter while resting. During spring, summer, and fall nights, dives were shorter, leading to the possibility that dolphins were resting at those times. The nonsurface feeding period corresponded with nighttime dispersal of southern anchovy schools. Dolphins moved in shallow water while resting and in deeper water while surface feeding. Near shore resting may be a predator-avoidance mechanism.

Most aerial behavior occurred during surface feeding, with behavior before and during surface feeding related to either herding and confining prey or possible communication of neighboring groups. Postfeeding aerial displays were assumed to serve a social function.

Calves were born mainly in the summer.

Recently there has been an increase in the number of studies of movements and migration patterns, behavior, and ecology of dolphins. Most of this work has consisted of long-term observations of the bottlenose dolphin, *Tursiops* sp. (Caldwell et al. 1965; Caldwell and Caldwell 1972; Tayler and Saayman 1972; Irvine and Wells 1972; Saayman et al. 1972, 1973; Saayman and Tayler 1973; Leatherwood 1975; Odell 1975, 1976; Castello and Pinedo 1977; Shane 1977; Würsig and Würsig 1977, 1979; Würsig 1978; Wells et al. in press; Irvine et al.[2]), but other odontocete cetaceans have received attention as well (review to 1974 by Norris and Dohl in press; Saayman and Tayler 1979, on *Sousa* sp.; Evans 1976, on *Delphinus delphis*; Norris and Dohl 1980, on *Stenella longirostris*; Gaskin et al. 1975, on *Phocoena phocoena*; Würsig in press, on *Lagenorhynchus obscurus*). This paper presents data on the yearly and daily occurrence and feeding cycles, movement patterns, general and social behavior, and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in a south Atlantic bay on the coast of Argentina.

Little information on dusky dolphins is available in the published literature. Gaskin (1968) described the distribution of these animals around New Zealand relative to sea-surface temperature, and Gaskin (1972) presented a summary of the literature. Although the genus *Lagenorhynchus* appears worldwide, populations of *L. obscurus* are confined to the Southern Hemisphere, most notably around New Zealand, South Africa, and South America. The exact northern and southern limits of the species are not known. Brownell (1965) states that dusky dolphins are distributed circumpolar to lat. 30° S, but this is disputed by Gaskin (1972). According to Rice (1977), *L. fitzroyi* is synonymous with *L. obscurus*.

More information is available on the Pacific whitesided dolphin, *L. obliquidens*. It has been described by Brown and Norris (1956), Norris and Prescott (1961), and others. A recent review of the status of this species in the eastern North Pacific

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[2]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Final report for U.S. Marine Mammal Commission, Contracts MM4AC004 and MM5AC0018, 53 p.

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has been presented by Leatherwood and Reeves (1978).

MATERIALS AND METHODS

Dusky dolphins were observed at Golfo San José (Figure 1) from September 1973 through January 1974 and from July 1974 through March 1976. We made observations from shore and from a 4.5 m rubber Zodiac[3] boat powered by an 18-hp Evinrude outboard motor.

Shore observations were made through binoculars, and movement patterns of dolphin groups, ranging from six to several hundred individuals, were followed with a Kern Model DKM 1 surveyor's theodolite (see Materials and Methods in Würsig and Würsig 1979). This technique allowed us to describe where and how fast the dolphins moved during different times of day.

Observations were made from the boat by moving up to a group of dolphins and then stopping the engine. This allowed us to drift near the dolphins while taking notes on their behavior. We believe that the natural behavior of dolphins was at times affected by the presence of the boat, and therefore made an attempt to confirm all behavior seen from the boat by shore-based observations.

To get some idea of group stability over time, we spaghetti-tagged 24 individuals in conjunction with a radio-tagging study. These tags were color-coded plastic streamers lanced into the thick blubber behind the dorsal fin. For a description of the tags and tagging procedures, as well as radio-track data, see Würsig (in press).

To compare seasonal occurrence data with water temperature, we measured temperature 1 m below the surface 5-10 times per month. For uniformity, these readings were made 0.5-3 km from shore, and in the afternoon. We used a calibrated laboratory thermometer marked every 0.2° C from 5.0° to 30.0° C.

Underwater sounds made by dolphins were recorded through U.S. Navy Sonabuoy hydrophones suspended 5-10 m below the boat. They were recorded on a Sony TC800B reel-to-reel tape recorder. A complete analysis of dolphin vocalizations is not presented in this paper. However, measurements were made of approximate distance of travel before attenuation (sounds no longer picked up by the hydrophones) of certain splash sounds related to aerial behavior. During such measurements, dolphin and boat position were recorded from shore by surveyor's theodolite, thereby providing the distance from the sound source to the hydrophone.

We used standard statistical techniques to test for differences and similarities of observations. These techniques are from Sokal and Rohlf (1969) unless stated otherwise.

RESULTS

Seasonal Occurrence Pattern

On days with winds >20 km/h, it was difficult to see dusky dolphins. Of the 433 days with winds <20km/h, dolphins were seen on 251 days, or 58%. Dolphins were seen from shore during 19 of 21 mo (Figure 2a); June and July 1975 were the only months without sightings. Although the rate of sightings varied from month to month, there was an increase in sightings from late winter (August) to summer (February 1975; December 1975), and a decrease from fall to midwinter (March through June 1975). During both years, dolphins were present on over 50% of days during which observations were made from August through February, with the one exception of <50% on the days in January 1976.

Could this cycle of dolphin occurrence be related to water temperature? Figure 2b shows average surface temperature per month within 3 km of shore during the same 21-mo period. Although upon superficial examination it appears that dolphins were less often present during the coldest months, this is not strictly true. Thus, although August was the coldest month in both years, dolphins in August were present over 70% of sighting days. The rise in temperature in spring-summer 1975-76, however, occurred earlier than in 1974-75, and temperatures from September to February were 1°-2° C higher per month than in the preceding year. Dolphins were more abundant earlier in 1975-76 than in 1974-75. While "the peak" of dolphin presence occurred in January 1975, it occurred in October 1975 in the next season, with a sharp drop-off to January 1976.

Where were the dolphins during the period from March through July, when they were rarely sighted in the study area? During 19 of 24 (79%) boat trips made throughout the bay in these months, we found them in the western part of Golfo San José, closer to the mouth of the bay and

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

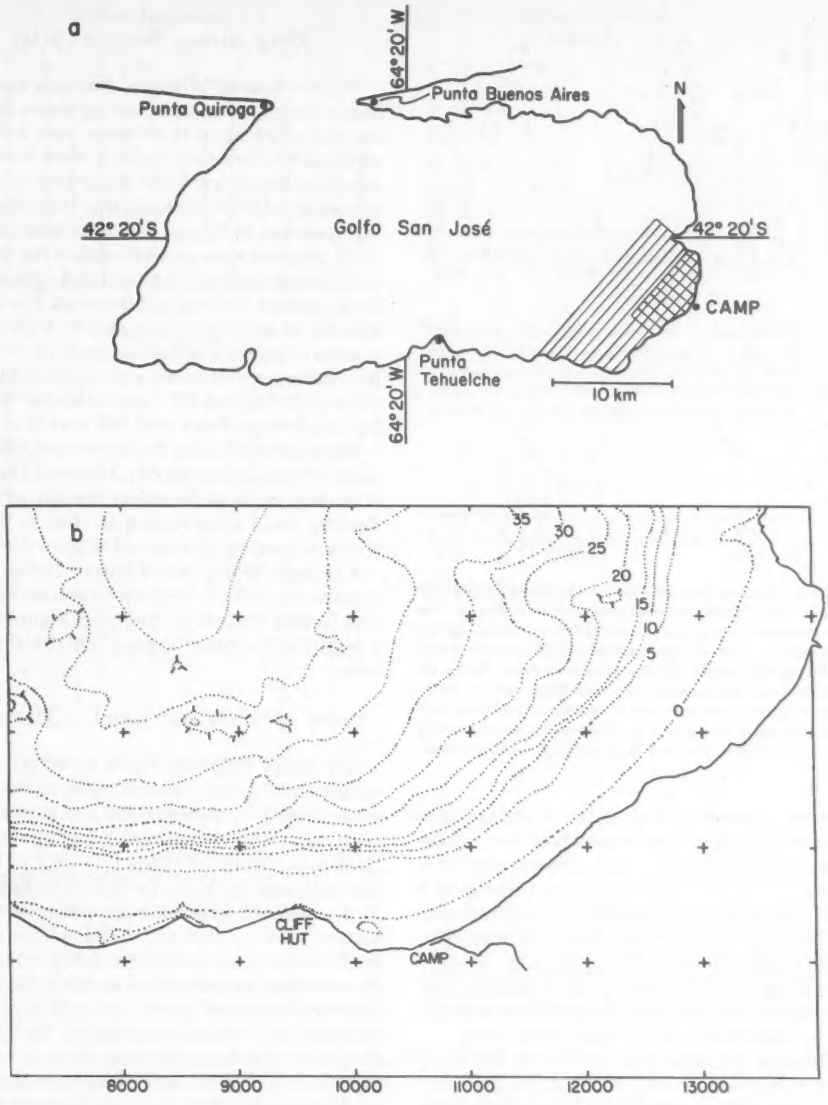

FIGURE 1.—Map of Golfo San José on Peninsula Valdés, Argentina (a). The bay is about 750 km² in area, with a 7 km wide mouth opening to the Atlantic. The lined area in the southeast portion of the bay represents the study area. The crosshatched subsection is shown in detail in b. It is a depth contour map of one-fourth of the study area. Margin numbers represent meter distances relative to a zero location on land. Crosses form 1 km squares. "Cliff Hut" and "Camp" are the locations from which most observations were made. Depth contours are in meters at mean low water (MLW). The usual distance for good observation of a moving dolphin group was at least 3 km. At a normal tide height of 5 m above MLW, water depth of 40 m was 1 km from Cliff Hut, and thus clearly visible. The map is from a larger area map which was by courtesy of Roger Payne, New York Zoological Society; Oliver Brazier, Woods Hole Oceanographic Institute; and Russ Charif, Harvard University.

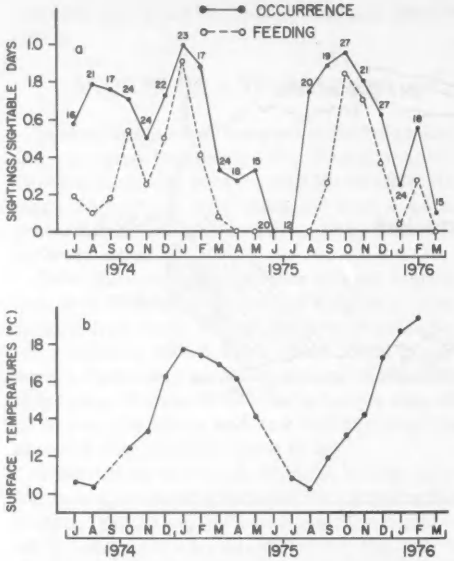
OCCURRENCE
FEEDING
SIGHTINGS/SIGHTABLE DAYS
a
J A S O N D J F M A M J J A S O N D J F M
1974
1975
1976
SURFACE TEMPERATURES (°C)
b
J A S O N D J F M A M J J A S O N D J F M
1974
1975
1976

FIGURE 2.—Fraction of possible days per month on which dusky dolphins were sighted, and were seen surface feeding (a). The y-axis represents the ratio of number of days on which dolphins were sighted or were seen feeding divided by the number of days each month with winds <20 km/h (sightable days). During all sightable days, observations were made from dawn to dusk. Numbers above points represent the number of sightable days per corresponding month. Average surface temperatures within 3 km of shore during the same 21-mo period as in Figure 2a(b).

near the open ocean (Figure 1a). A large oceanic mass of water changes temperature less rapidly than nearshore shallow water, and this may have influenced the dolphin's movement, perhaps by a shift in prey location. Dolphins were found near the mouth of the bay from March through July, when temperatures in the study area dropped from 17° to 11° C (Figure 2), and it is likely that near-mouth temperatures decreased more slowly due to the influence of the open ocean water.

Although dolphins were present at the study site most of the year, and were found in Golfo San José the entire year, we did not know whether the animals were part of the same population or herd during all seasons. However, four spaghetti tags inserted in December and January were resighted in August, November, December, and January of subsequent years. This indicated that at least some of the animals were present in different seasons, and thus did not appear to migrate.

Seasonal and Daily Surface Feeding Cycles

Surface feeding of dusky dolphins was often highly visible, with birds flocking above the feeding site, allowing us to estimate from a distance when and where the dolphins were feeding on schooling fish (Figure 2a). Regardless of season, whenever dolphins were seen they were often feeding. However, in August and September 1974 and 1975, dolphins were present much of the time but little surface feeding appeared to take place. Little or no surface feeding took place in low-dolphin months of June and July and in high-dolphin months of August and September. This low in surface feeding corresponded with the lowest temperature period (about 12° C and below) of the year, possibly because fewer food fish were in the area.

When surface feeding bouts occurred, they were observed throughout the day. However, the length of feeding bouts increased as the day advanced. Feeding bouts were longest at 1500 h, then declined as evening approached (Figure 3).

Although feeding lasted longer during the afternoon (to 1500 h), there were nevertheless some long feeding bouts in the morning (Figure 4), with a significant increase in long bouts in the afternoon.

Depth of Water and Speed of Movement

Are dusky dolphins found at certain water depths and does their swimming speed vary with water depth? To answer these and similar questions, we tracked group movements by surveyor's theodolite. Figure 5a shows that they were most often tracked while in water 5-10 m deep. This peak is probably somewhat biased because observations were possible more often within about 1 km from shore, where depths of 0-30 m were found. Nevertheless, since both 0-5 m and 10-30 m depth areas approximated the area at 5-10 m, dolphins appeared to have a clear preference for traveling in water 5-10 m deep while near shore. A small but significant secondary peak also occurred at 35-45 m. Although dolphins traveled in water >65 m, this has not been represented in Figure 5a, since no water within sight was >65 m. For radio tracked movement out of sight of land see Würsig (in press).

The overall average speed was 7.7 km/h. There was a shift in speed depending upon depth of water in which the animals were traveling (Figure 6).

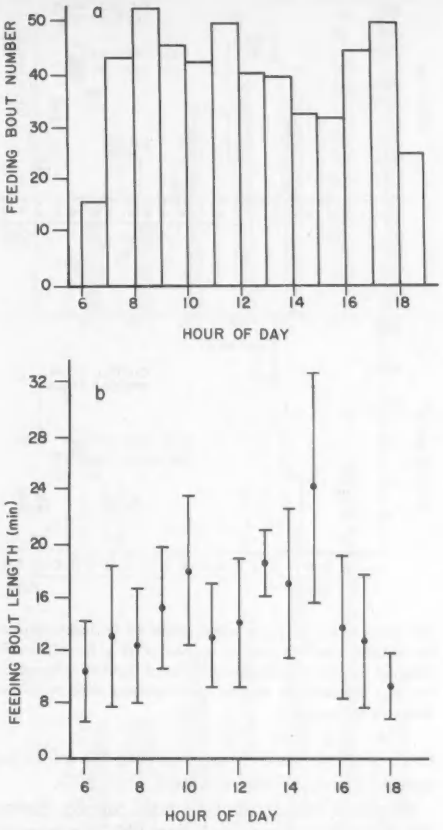

FIGURE 3.—The number (a) and mean lengths (b) of dusky dolphin feeding bouts throughout the day, summed for 21 mo from June 1974 to March 1976. Bars above and below mean feeding lengths enclose 95% confidence intervals for means.

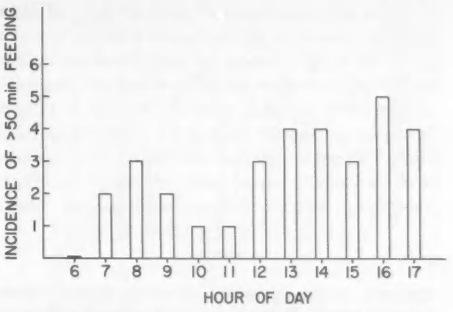

FIGURE 4.—The number of >50-min surface feeding periods of dusky dolphins during different times of day. Significantly longer surface feeding periods occurred in the afternoon (0600-1200 h = 9 or 28%; 1200-1700 h = 23 or 72%; testing equality of percentages, arc sine transformation ofr statistic t_s).

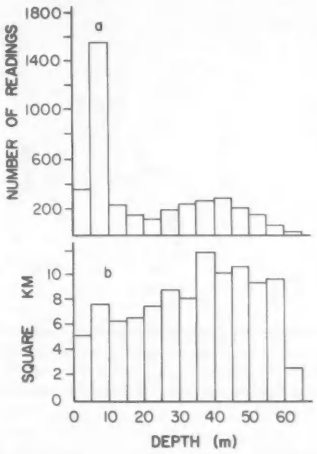

FIGURE 5.—Number of theodolite readings of dusky dolphins over depths from 2 to 65 m (a). Although most readings were at 5-10 m, a smaller peak occurred at 35-45 m which appeared to correlate with feeding activity at that depth (see text). Amount of area available in the study region as a function of water depth, at a mean tide height of 5.0 m above mean low water (b).

Groups moved at about 5 km/h in water 1-10 m, and faster in deeper water (average speed in water 55-60 m was 16 km/h). Furthermore, there was a general movement from shallow to deeper water as the day advanced (Figure 7a), and dolphins moved more rapidly in the afternoon than in the morning (Figure 7b).

Because water depth and dolphin speed were related (Figure 6), it is not surprising that dolphins, on the average, moved faster in those months in which they were in deeper water (compare Figure 8a with b). At the same time there was a strong correlation between depth and speed during different months and the amount of feeding activity during those months (compare Figure 8a with Figure 2a; correlation = 0.77, $P = 0.003$, Kendall coefficient of rank correlation).

Dolphin groups moved into deeper water in the afternoon in each of the 7 mo for which adequate depth versus time of day data exist (Figure 9a). In August and September, when little surface feeding occurred, and when water temperatures were lower than in summer, dolphins stayed in rela-

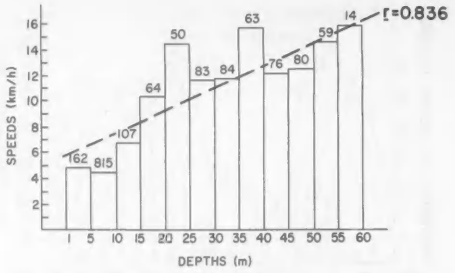

FIGURE 6.—Average speeds with which dusky dolphins traveled at different depths. The least squares regression, fit to the means shown, is statistically significant ($P<0.01$). Numbers over bars represent number of observations in that category.

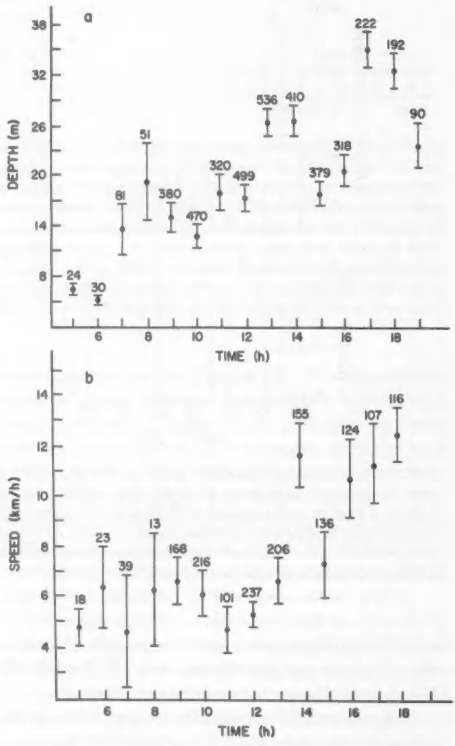

FIGURE 7.—Mean depth of water (a) and mean swimming speed (b) of dusky dolphins as a function of time of day. Bars represent 95% confidence intervals for means and numbers above bars represent the number of theodolite readings per hour interval.

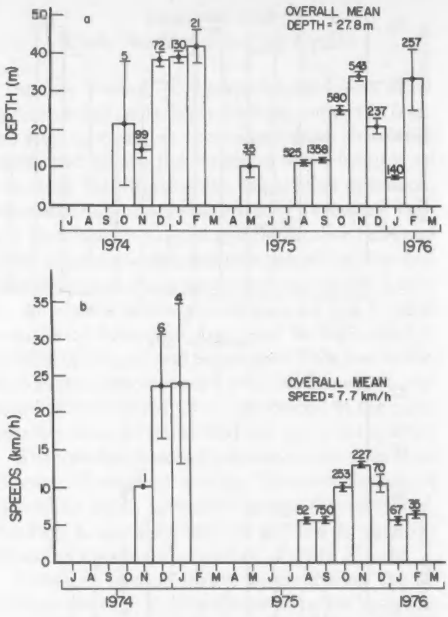

FIGURE 8.—Mean depth of water inhabited by dusky dolphins for different months (a), and mean speed of travel for dolphins for different months (b). Numbers represent number of theodolite readings obtained per month; bars represent 95% confidence intervals for means.

tively shallow water compared with the following months (Mann-Whitney U-test, $P<0.001$).

Dolphins usually moved more rapidly during afternoon than morning (Figure 9b). The increase in rapid movement per month appears related to the amount of surface feeding bouts in that month. Thus, in August 1974 and 1975 few surface feeding bouts occurred, and there was no increase in speed during the day. In September, some feeding took place, and there was a small speed increase. In October, November, December, and January much surface feeding took place during one or both years, and the afternoon speed increase was most dramatic. In February, both surface feeding and afternoon speeds were again down to pre-October levels (August, September, and February afternoon speeds are significantly different from October, November, December, and January afternoon speeds, Mann-Whitney U-test, $P<0.001$).

From these data we concluded that dolphins traveled faster at surface feeding times. This was confirmed by comparing speed data of dolphins as

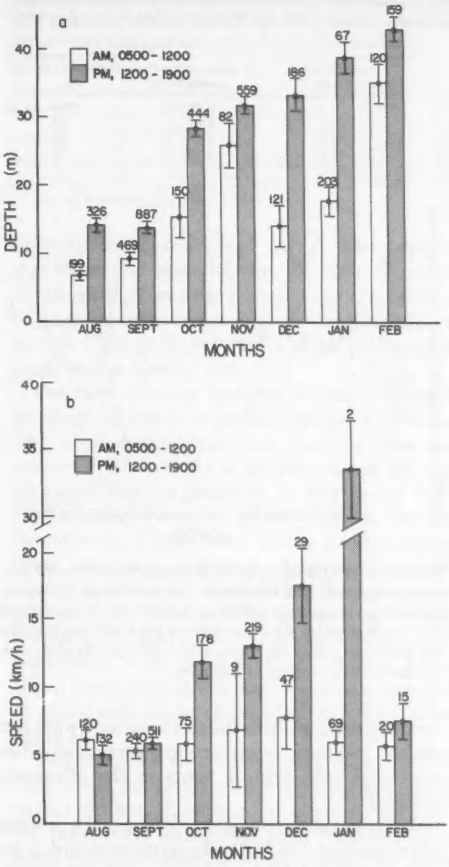

FIGURE 9.—Mean depth of water (a) and mean speed (b) of dusky dolphin travel in mornings versus afternoons, separated into those months for which adequate data are available. The lines above and below bars represent 95% confidence intervals for means, and numbers represent number of theodolite readings. During August and September, dolphins were found in significantly shallower water than during the spring and summer months of October-February (Mann-Whitney U-test, $P<0.001$). During August and September, dolphins also moved significantly slower than October through January (Mann-Whitney U-test, $P<0.001$). Almost all speed increases in these months took place in the afternoon.

they moved with no feeding bouts present in the area, and as they moved near feeding bouts (Table 1). The mean speed without feeding bouts was 6.3 km/h, while speeds around feeding bouts averaged about 15 km/h.

Dusky dolphins spent more time in deeper water when surface feeding. Furthermore, the depth of water in which surface feeding occurred increased as the summer season advanced (Figure 10). Thus the mean depth of feeding bouts during September was 21 m, but by February dolphins were surface feeding in waters 41 m deep. Since it is a general rule (and confirmed for Golfo San José by Pizzaro (1976), and pers. obs.) that deeper offshore water is cooler than shallow nearshore water in summer,

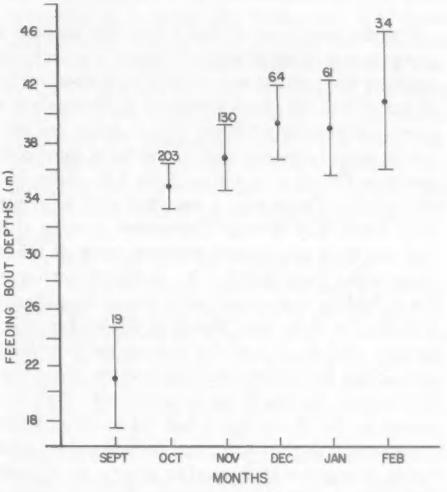

FIGURE 10.—Mean depth of dusky dolphin surface feeding bouts during different months. Bars above and below means represent 95% confidence intervals for means. Numbers above bars represent the number of theodolite readings of feeding bouts per month.

this change in preferred feeding locations may represent a change in movement patterns of fish upon which the dolphins were feeding. We caught fish from schools on which the dolphins were feeding on 15 separate occasions, and identified the species composing such schools in the field about 50 more times. In all cases, the fish were southern anchovy, *Engraulis anchoita*. These fish are found in deeper water during summer in a nearby coastal area, where they are netted by fishermen (Mermoz[4]), and we suspect that they move into deeper water in summer in the present study area as well.

[4]J. Mermoz, research scientist, Museo de Ciencias, Buenos Aires, Argentina, pers. commun. 1975.

TABLE 1.—Average speeds of dusky dolphins not associated with feeding, and associated with feeding activity. The difference in speed between no feeding activity seen (row 1) and speed around feeding activity (rows 2, 3, and 4) is significant ($P<0.001$, t'-test of equality of means when variances are assumed to be heteroscedastic).

Row	Category	Average speed (km/h)	Standard deviation	Theodolite readings (n)
1	No feeding activity seen	6.3	2.35	1,390
2	Dolphins not associated with feeding activity in the area	15.3	3.46	72
3	Movement towards feeding activity	13.7	3.43	88
4	Movement out of feeding activity	15.6	3.52	109

Relationships of Group Sizes, Feeding, and Aerial Behavior

For the purposes of this paper, we defined a group as a number of animals that are swimming together and moving as a unit (but not necessarily all pointed in the same direction). Individuals of a group were usually within visual range and certainly within acoustic range of at least some conspecifics. Group sizes varied from 6 to about 300 individuals. There was a seasonal shift in group sizes. From May through September, groups with <20 animals were more common than at other times of the year (Figure 11). As stated earlier, a low in feeding bouts occurred in the southeast part of Golfo San José from March to September (Figure 2a), and we gained the impression from boat trips to the middle and western section of the bay that surface feeding there occurred with high frequency in March and April, but did not often occur anywhere in the bay from May to September. As a result, it appears that smaller groups were most abundant during the nonsurface feeding months of May to September.

There was a direct relationship between size of dolphin group and surface feeding frequency. Thus, groups with <20 individuals were found in feeding bouts only 19% of the times they were spotted, while groups with >20 animals were seen feeding more of the time (Table 2). Because a surface feeding-speed relationship was noted, it is not surprising that speed of group travel increased with increasing group size. While small groups occurred most often in the morning (and were not surface feeding), larger groups were most often associated with feeding bouts in the afternoon (Table 2).

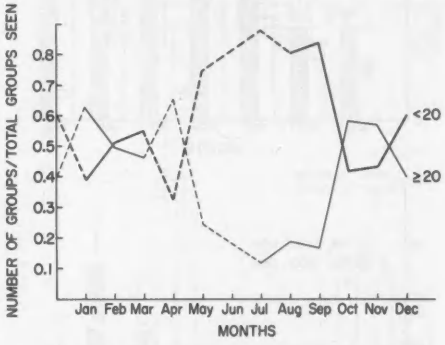

FIGURE 11.—Percentage of dusky dolphin groups with <20 individuals compared with those with ≥20 individuals, by month. Dashed lines connect one or both points with <10 groups sighted that month. October-April percentages are significantly different from those of May-September ($P<0.001$, equality of percentage test with arc sine transformation).

The larger the group size, the longer the feeding activity lasted (Table 3). The number of birds also increased with dolphin group size, and with length of feeding (Table 3). Species of birds, in approximate order of decreasing numbers, were the black-headed gull, *Larus dominicanus*; cormorants, *Phalacrocorax brasilianus* and *P. magellanicus*; terns, *Sterna* spp.; different species of Pro-

TABLE 2.—Average speed and time of day related to group size estimates, and percentage of times dusky dolphins of three different group sizes were associated with feeding activity. Groups with <20 individuals were seen feeding less frequently than larger groups ($P<0.001$, testing quality of percentages, arc sine transformation of t-statistic).

Item	Dolphin group size (estimate) <20	≥20<50	≥50
Number of theodolite readings used for speed data	66	37	30
Average speed (km/h)	5.7	7.4	13.8
Standard deviation	2.30	2.60	3.45
Average time of day, Argentine local time (h:min)	10:12	13:20	14:06
Standard deviation expressed in hours and minutes	2:40	2:57	2:45
Number of times seen feeding (a)	130	177	190
Number of times seen while not feeding (b)	540	117	77
Percentage of times seen feeding during total sightings (100a/(a + b))	19	60	71

TABLE 3.—Estimated number of dusky dolphins and birds (see text) in feeding bouts of different lengths (t'-test of equality of means when variances are assumed to be heteroscedastic).

Dolphin group size	Mean length of feeding by dolphins			Mean number of birds		
	n	Mean[1]	SD	*n*	Mean[1]	SD
<10	19	6.3ns	4.42	19	75*	73.8
≥10<20	91	11.1**	12.00	91	115**	82.3
≥20<50	116	16.5**	14.38	116	163**	116.5
≥50	87	25.8	24.23	87	246	117.8

[1]ns = not significant; *$P<0.05$; **$P<0.01$.

cellariiformes; the giant petrel, *Macronectes giganteus*; and black-browed albatross, *Diomeda melanophris*. Terns were usually the first birds to begin flying over and diving into feeding dolphin groups. Then gulls and finally larger birds aggregated at the feeding area.

The most striking behavior of dusky dolphins we observed was their aerial displays. To find out why these displays occurred, we noted the frequency of this activity at different times. We saw all aerial displays described by Norris and Dohl (1980) for the Hawaiian spinner dolphin, *Stenella longirostris*. These were leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, spins, and noseouts. The most "acrobatic" of these leaps was the head-over-tail leap. The spin was performed frequently by the Hawaiian spinner dolphin, but it constituted <1% of leaps in the present study. When it was seen, it was also classified as acrobatic, along with the head-over-tail leap, for further analysis.

Two other aerial displays seen in dusky dolphins were the headfirst reentry leap and its apparent variant, "humping." In the headfirst reentry, the dolphin leaped clear of the water and then arched its back strongly while flipping the tail to make a headfirst reentry. While humping, the same motion occurred except that the snout and tail did not leave the water during the body arch.

Leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, and spins usually occurred in groups. That is, one animal started a particular leap, and then continued it from 3 to about 20 times. Because we could often not be certain that the same individual was performing the leaps during a leap sequence, we do not have complete quantification for this phenomenon. However, in 45 of over 1,000 leaps it was certain that the same animal leaped throughout a sequence, because we followed it visually while it swam below the surface between leaps. In all 45 instances, the leap type per sequence did not change, and a mean of 4 (SD = 2.2) leaps per sequence was performed. Although the first five or so leaps were performed with "exuberance," as animals leaped clear of the water and reentered forcefully, successive leaps were not as high, possibly as the animal tired.

The headfirst reentry and humping did not occur in sequence, but were usually performed only once by an animal within about 30 s. Because animals stayed underwater for long times between leaps, we could never be certain that the same animal leaped later on. Instead, the 30-s estimate was derived from counts of total leaps occurring in a particular group size, and must therefore be treated with caution. The headfirst reentry and humping were often performed in concert with one or two others leaping in the same manner at the same time. While all other aerial behaviors left individuals close to the water surface between leaps, the headfirst reentry and humping took them farther below the surface, and we saw them swimming out of sight at about a 75° angle.

As was described by Norris and Dohl (1980), leaps, head-over-tail leaps, backslaps, headslaps, tailslaps, and spins made noise as the animals reentered the water. That is, they created sharp bursts of sound when the animals slapped the water with their flukes or body upon reentry. Hydrophones detected the sounds underwater at approximately 0.5 km distance, but not at 1.0 km distance during four recording sessions under optimal (no wind or waves) conditions. Norris and Dohl also mentioned that sounds made by these leaps attenuate relatively rapidly, but gave no distance estimates.

Headfirst reentry and humping, however, made little or no sound above or below the water (hydrophones did not detect sound 10 m from the activity). Dolphins slid out of and into the water along their longitudinal body axis during these two leap types. Because we believe that the noise made by most leaps may be biologically meaningful, we separated them into "plain noisy" (the leap, backslap, headslap, and tailslap) and "acrobatic noisy" (head-over-tail and spin) leaps, and distinguished them from noiseless or "clean" leaps (headfirst reentries and humping). The noseout did not make noise and was often difficult to see from the boat or from shore. It was therefore not quantified.

We observed dolphins in feeding bouts for 145 h, and observed them during periods when we saw no feeding bouts for 309 h, or over twice as long. Nevertheless, we saw a significantly higher fre-

quency of noisy and clean leaps while dolphins were surface feeding (Table 4). More noisy leaps were made during and after surface feeding than before, and those few noisy leaps which occurred before surface feeding were most often "plain" or nonacrobatic. During surface feeding, plain and acrobatic leaps occurred with about equal frequency, while after surface feeding most leaps were acrobatic. The noiseless or "clean" head-first reentry leap and humping behavior occurred more often before and during surface feeding than after surface feeding.

Our general views of behavior introduced above were as follows: When not surface feeding, dolphins usually moved in small (<20 individuals) groups (Table 2) with sporadic but relatively infrequent aerial behavior (Table 4). They usually moved slowly (about 6 km/h) at this time. Immediately previous to feeding bouts, they moved more rapidly for short periods (mean time = 6.2 min, SD = 4.53), often creating whitewater as they surged through the water at speeds >10 km/h (Table 1). We gained the impression that between such surges, they stayed underwater for longer periods than their normal diving times (mean dive time = 21 s, Würsig in press), often disappearing from sight for over 60 s. This pattern of movement lasted from a few minutes to as long as 1 h. When it stopped and dolphins were again found more often near the surface, they moved slowly and stayed in basically the same location. At this time, noiseless (clean) and noisy (plain) leaps began (Table 4). When we were near this activity in a boat, we were able to see a fish school usually 2-3 m in horizontal diameter, and 0.5 m vertical height, near the water surface.

Every time (65 occasions) the fish were observed they were southern anchovy 6-15 cm long. When we spotted the fish school near the surface, we also saw terns beginning to dive for the fish, and gulls coming from the vicinity. Plain noisy and clean leaps continued, and acrobatic leaps began to appear (Table 4). During surface feeding, many of the clean displays were composed of humping behavior. During humping, dolphins rapidly moved singly or in pairs through the fish school after coming almost vertically from deeper water, caught one to five fish in their mouths, and then descended again at a steep angle. Dolphins were also seen near and around the feeding bout nucleus, chasing and feeding on individual fish not part of the tight school.

If the surface feeding dolphins were not joined by a nearby group or groups within several minutes, the feeding bout died down. We lost sight of the fish, either because the school had been reduced by dolphins and birds or because it moved away from the surface. Often, however, other dolphin groups in the vicinity converged on the feeding bout, moving rapidly in a straight line towards the feeding birds and dolphins from as far away as 8 km, measured by theodolite on one occasion. A more usual distance was 2-3 km. As a result of this movement, the feeding bout grew larger—up to an estimated 300 dolphins and thousands of birds—and lasted for a correspondingly longer time (Table 3). Surface feeding appeared to stop when dolphins rapidly moved away from the activity, or when they began deep dives and clean leaps once again. In either case, we no longer saw the fish school. Birds stopped flying and diving in a concentrated area and settled on the water or followed

TABLE 4.—Observed incidences of aerial behavior in dusky dolphins. Numbers represent number of 15-min periods during which a particular type of leap was seen. Frequency of leaping within that period has not been quantified. "Noisy leaps, in general" represent leaps which made noise but were not separated into "plain" or "acrobatic" during data gathering. All significance testing used the equality of percentages, arc sine transformation for the statistic t_s.

Time of leaping	a Noisy leaps, in general	b Plain noisy leaps	c Acrobatic noisy leaps	d Clean leaps
A During the 15 min before feeding	24	17	0	35
B During feeding (average time of 15 min)	109	13	15	32
C During the 15 min after feeding	84	1	20	12
D Without feeding	45	22	3	25
Total	262	53	38	104

Comparisons:
Amount of noisy leaps, in general, a, associated with feeding, A-C (83%) versus without feeding, D (17%); significant difference, $P<0.001$.
Amount of noisy leaps, in general, a, before feeding, A (22%) versus after feeding, C (78%); significant difference, $P<0.001$.
Amount of noisy leaps before feeding, A, plain, b (100%) versus acrobatic, C (0%); significant difference, $P<0.001$.
Amount of noisy leaps after feeding, C, plain, b (4.8%) versus acrobatic, D (95.2%); significant difference, $P<0.001$.
Amount of plain noisy leaps, b, before feeding, A (94.4%) versus after feeding, C (5.6%); significant difference, $P<0.001$.
Amount of acrobatic noisy leaps, c, before feeding, A (0%) versus after feeding, C (100%) significant difference, $P<0.001$.
Amount of clean leaps, d, associated with feeding, A-C (76%) versus without feeding, D (24%); significant difference, $P<0.001$.
Amount of clean leaps, d, before feeding, A (74%) versus after feeding, C (26%); significant difference, $P<0.01$.

the rapidly moving dolphin group. Dolphins tended to stay together for up to several hours once groups had converged to feed, and feeding activity usually started again in these larger groups. When it did so, it lasted longer than when fewer dolphins were feeding, and therefore larger groups were more often seen in association with feeding bouts (Table 2).

Group Organization and Calving Periodicity

As mentioned previously, the most common nonfeeding group size was about 6-15 animals. In general, these groups were composed of adults, and at times included juveniles and calves. We were not able to determine sex of individuals by observing them from boat or shore, but captures of individuals prior to radio tagging (Würsig in press) demonstrated that males and females usually travelled together in these small groups. We saw small calves (about equal to or less than one-third adult size) from November through February. Furthermore, we saw "juveniles" (about one-half to two-thirds of the size of adults) or young under 1 yr of age during April-May and August-September (Table 5). The sample size was too small, however, to say definitely that young were born only during the summer, and births may have been more spread out over the year. Nevertheless, the data suggest a summer calving peak.

Although we saw small calves and young in small groups, we also saw groups of 8-20 adults and as many calves on six separate occasions. We called these groupings "nursery" groups, on the assumption that the adults may have been females, and the calves their young. During all six sightings of nursery groups, most or all other animals in the vicinity were engaged in feeding activity and aerial behavior 0.5 to several kilometers distant from the nursery group. During 12 other sightings of calves and adults, they were found in small groups in the ratio of approximately 1 calf to 10 adults and were not engaged in large-group feeding activity (although on 3 of the 12 occasions, we saw calves in small groups that were feeding). We suspect from these observations that young normally travel with adults in small groups, but when many groups coalesce to feed and socialize (see below), calves and certain adults split off at some time and form temporary nursery groups.

If there is a calving peak during the year, then most successful matings are probably also carried out in a relatively restricted time period. Most apparent copulations, consisting of rapid belly-to-belly swimming and frequent pelvic thrusts by one or both animals, appeared to take place in large groups during and after surface feeding. Most of these large groups were found in summer (Figure 11). However, it was difficult to approach small, nonsurface feeding groups, and we have few data on their underwater behavior and possible mating attempts. Although we saw some apparent mating in groups of all sizes and at all times of the year, we were not able to quantify these observations.

When we saw small groups of 6-15 animals, we usually saw many of them, up to about 30 such groups, in an area approximately 10 km in diameter. However, we were able to count these groups only under the best conditions, on a calm sea. When these groups converged to surface feed, the upper limit of group size estimate was 300 animals, and this estimate—made by different observers and at different times of year—did not vary appreciably. It thus appears that small groups made up part of a larger school or herd of animals. We do not know how stable small groups were over time, although evidence has been presented by Würsig (in press) which suggested that at least some groups remained stable over a period of at least several days, and appeared to remain together in "subgroups" of a large group during and after feeding bouts.

TABLE 5.—Sightings of calves and juvenile dusky dolphins. Incidence of calves during November to February was significantly higher than in the rest of the year ($P<0.001$, Raleigh test, Greenwood and Durand 1955).

Month	Number of sightings		Month	Number of sightings	
	Calves	Juveniles		Calves	Juveniles
Jan.	4	0	July	0	0
Feb.	1	0	Aug.	0	2
Mar.	0	0	Sept.	0	2
Apr.	0	1	Oct.	0	0
May	0	1	Nov.	2	0
June	0	0	Dec.	3	0
			Total	10	6

Interspecific Interactions

Dolphins associated with the boat at times by rapidly moving towards a moving boat from as far as 2-3 km. They would then ride the bow and stern pressure waves of the boat in characteristic dolphin fashion. This activity took place mainly when the dolphins had been surface feeding for a long

time and were thus in large groups. Table 6 shows a few instances of this behavior, when we were certain whether or not the dolphins had been feeding. The data confirm the impression that dolphins which had been in or near feeding bouts approached the boat, while groups which had not been surface feeding avoided or ignored it. When the dolphins associated with the boat, a high level of acrobatic noisy leaps was also evident. Of course, it is likely that the dolphins were merely associating with the boat, and that the humans on board were irrelevant.

Dolphins also associated with the southern right whale, *Eubalaena glacialis*, and the sea lion, *Otaria flavescens*, by moving around and among them in a manner similar to that described for bottlenose dolphins (Würsig and Würsig 1979). This activity also appeared related to whether dolphins had or had not been surface feeding. Differences in behavior between "fed" and nonfeeding dolphins were striking, and we labeled them different "activity levels," following the definition of this term by Norris and Dohl (1980).

After feeding, dolphins at times balanced kelp (pieces of *Macrocystis* sp.) on their pectoral flippers. In one individual this persisted for at least 1 h. The activity of kelp-balancing, we suspect, may be termed "play."

Dolphins interacted with other odontocete cetaceans as well. Groups of from one to six killer whales, *Orcinus orca*, appeared for brief periods throughout the year (Table 7). On the six occasions when we saw them within about 1 km of dusky dolphins, the dolphins moved rapidly in a tightly bunched group away from the killer whales. On three occasions when dolphins were within 1 km of land, they moved towards the shore, and then proceeded along shore in water less than 1 m deep, the closest to shore we ever saw this species. It was reported to us by reliable observers (Jen and Des Bartlett[5]) that killer whales in our study area once surfaced within a school of dusky dolphins, with one whale dripping blood from its mouth, perhaps indicative of having actually fed on a dolphin. However, we have no conclusive evidence that killer whales habitually feed on dusky dolphins.

Risso's dolphin *Grampus griseus*, associated with dusky dolphins from October through March 1974-75 and 1975-76 (Table 7). From two to six individuals consistently stayed within 1-3 km of feeding dusky dolphins during this time. It is possible that Risso's dolphins were feeding on large fish found in the vicinity of southern anchovy, but we have no data for this assumption. Whether or not the larger cetaceans were of actual help to dusky dolphins in finding food, as has been suggested by Norris and Prescott (1961) for pilot whales followed by bottlenose dolphins, and by northern right whale dolphins, is not known.

The bottlenose dolphin, *Tursiops truncatus*, was found in small groupings of 8-22 animals in the study area (Würsig 1978). They usually stayed in shallower water than did dusky dolphins, and were never observed moving in water >39 m. There was, however, some overlap in area covered by both species. On only eight occasions were both species found within 0.5 km of each other. When they were relatively close, each species continued on its previous course, and no interactions appeared to take place (although they may have been interacting by sound). This apparent lack of interaction was especially striking because both dolphin types associated with right whales and sea lions. Dusky dolphins were more abundant when bottlenose dolphins were not, and vice versa (Figure 12).

TABLE 6.—Number of times that dusky dolphin groups associated with the boat by orienting towards it and "bow riding," and number of times they avoided or ignored the boat; both relative to feeding activity (A significant difference from C, $P<0.01$; B significant difference from D, $P<0.001$; chi-square goodness of fit test).

Category	Moved to boat		Ignored boat	
Group not seen surface feeding	A	10	B	18
Group seen surface feeding previously on same day	C	28	D	1

TABLE 7.—The number of days per month when *Grampus griseus* and *Orcinus orca* were seen in the Golfo San José study area.

Month	*Grampus griseus*	*Orcinus orca*	Month	*Grampus griseus*	*Orcinus orca*
Jan.	6	2	July	0	0
Feb.	12	2	Aug.	0	0
Mar.	15	2	Sept.	0	3
Apr.	0	3	Oct.	7	0
May	0	1	Nov.	0	2
June	0	1	Dec.	5	5

DISCUSSION

Dusky dolphins were present in Golfo San José during most or all of the year, but were located in the southeast portion, in the study area, mainly during spring and early summer. They did not

[5]Jen and Des Bartlett, wildlife photographers, P.O. Box 17323, Tucson, AZ 85731, pers. commun. November 1974.

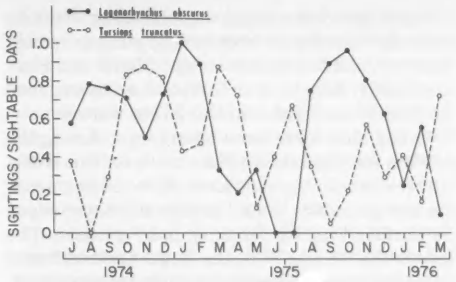

FIGURE 12.—Occurrence data from Figure 2a in conjunction with comparable data on bottlenose dolphins during the same period. The two species occurred in the study area with approximately opposite frequency, i.e., when one species was abundant, the other one was less often seen.

appear to avoid low (≈10° C) temperatures, but may have been avoiding higher (>18° C) temperatures near shore in mid- and late summer. At those times, they were found most often in cooler waters near the mouth of the bay. In Würsig (in press), it was shown that during that time they moved outside of the bay as well. Yet they did not show a well-defined seasonal migration pattern, and marked individuals were resighted in the same location during different seasons. Studies of groups of *Tursiops* sp. have indicated that degree of migration may be different for different populations. For example, bottlenose dolphins off Cape Hatteras, N. C., migrate (Mead 1975), while those of our study site did not (Würsig and Würsig 1979). Shane (1977) and Irvine et al. (see footnote 2) reported localized seasonal movements of bottlenose dolphins in the Gulf of Mexico, with differences between their East Texas and West Florida study sites. Degree of seasonally related movement probably hinges on several environmental and ecological variables, but an important factor for dolphins in temperate waters may be food availability (suggested by Norris 1967, Evans 1971, and others). Thus it seems likely that dusky dolphins moved with the food supply most of the year. The main prey item appears to be southern anchovy and we have some evidence that it is found in deeper offshore waters in spring and summer (Ciechomski 1965) and in large concentrations near the mouth of Golfo San José in late summer (Brandhorst and Castello 1971), at the same time dusky dolphins were feeding there.

Gaskin (1968) stated that dusky dolphins are present around the Hawke Bay area of New Zealand generally only in winter and spring. He related this to the presence of the cold Canterbury Current which comes close to Hawke Bay in winter and spring. Clarke (1957) and Sergeant (1962) described the seasonal migration by pilot whales as being regulated mainly by seasonal abundance of squid and certain schooling fish. Wilke et al. (1953) also found seasonal movement patterns for the Dall porpoise, *Phocoenoides dalli;* the northern right whale dolphin, *Lissodelphis borealis*; and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens*. Norris and Prescott (1961) and Evans (1971) reported that the common dolphin, *Delphinus delphis,* moved closer to the shore of California in fall and winter, and moved farther offshore in spring and summer. They suggested that this movement was food related. Brown and Norris (1956) stated that whitesided dolphins off California were most often found near shore in winter and spring, and offshore in summer and fall. They also reported that the movements of the northern anchovy, *Engraulis mordax,* corresponded with the seasonal dolphin movements. Their observations of *L. obliquidens* thus agree with those of *L. obscurus* of the present study.

Frequency of feeding in the highly visible manner described, with birds flocking overhead, was seasonal. It occurred less often in winter than at other times. In winter, anchovy are found in water >100 m (which is deeper than Golfo San José), and farther north, around lat. 36°-37° S (Brandhorst et al. 1971). Thus it is probable that dolphins were not feeding on southern anchovy in winter in the study area. Yet it is not possible that mammals as small and as constantly active as dusky dolphins stopped feeding completely for several months. We can only guess that other feeding was done on prey below and not at the surface, and possibly more individually instead of as a concerted group effort. At any rate, in winter we observed very little aerial behavior and rapid movement usually attendant on surface feeding. Instead, dolphin groups consistently moved slowly and in small groups near shore. Stomach content samples would be helpful in solving this ambiguity.

Dolphins exhibited a daily feeding cycle as well. Morning surface feeding activity lasted for shorter times than in the afternoon, so that dolphins were more often seen feeding in the afternoon. They moved in shallow water (5-10 m) in the morning, but most afternoon surface feeding occurred in 35-45 m. We gained the impression that im-

mediately before feeding, dolphins were diving for longer periods, perhaps going down deep to hunt for food. This impression was not quantified in direct association with feeding because we were unable to identify particular individuals and thus obtain length of dive records. However, we have evidence from radio-tracked dusky dolphins indicating that there is a length of dive-surface feeding time association (Würsig in press). Dive times from six dusky dolphins radio-tracked in summer showed a consistent increase in length during afternoon, with average night and morning dives about 14 s. Noon and afternoon dives rose to as high as 32 s in average duration. One animal radio-tracked in the austral winter (July-August 1974) showed no such length of dive increase in the daytime and actually surfaced more frequently in the afternoon than at other times of the day and night. This is an indication that feeding in the winter was different from feeding in the summertime. Since we believe that long dives in summer are associated with surface feeding in deeper water, it is likely that the extremely shallow and brief dives which occurred at night (Würsig in press) in summer were not associated with feeding, and that perhaps the animals were resting near the surface much of the night. This is the reverse of what was found in the common dolphin off California (Evans 1971, 1974), which dives for long periods at night—and is believed to be feeding at that time—and dives relatively shallowly during the day. Once again, this difference may be food related. While the common dolphin is thought to feed upon the deep scattering layer which rises out of deeper water enough for the dolphin to dive to it at night, no defined deep scattering layer can exist in the relatively shallow nearshore waters of the present study (Hersey and Backus 1962). Instead, dolphins feed on anchovy during the day, and move into deeper water as the day advances. Whether or not anchovy move into deeper water and are followed by the dolphin is not known. Perhaps the daily movement into deeper water was simply a consequence of being in shallow, nearshore water during night and early morning (to be discussed later), and having to go into deeper water in order to feed more efficiently. It is known that individuals of southern anchovy schools disperse during nighttime (Brandhorst and Castello 1971). This dispersal may make nighttime feeding on anchovy more difficult or impossible, and therefore dolphins may rest at night while feeding during the day in summer.

As an apparent consequence of feeding, dolphins were also found more often in deep water in spring, summer, and fall than in winter. Norris and Prescott (1961) suggested a similar movement trend for *Delphinus delphis* in California waters.

Group sizes were more often larger during the surface feeding season. The reason for this was a direct relationship between surface feeding activity and group size. Small groups usually engaged in surface feeding for only brief periods. The longer the feeding bout, the larger the number of dolphins present. Dolphins appeared to begin feeding in the morning and continued feeding through most of the afternoon; thus, there was a general increase in group size as the day advanced. The many small groups in the morning (and presumably night as well) covered a large (up to about 10 km in diameter) area, but nearest neighbors were usually no more than 0.5 km apart. We assume that they were probably within acoustic range of each other. Why did surface feeding activity last longer when dolphin numbers increased as groups joined? Perhaps larger schools of fish attract more dolphins and keep them feeding for a longer time. It is also possible that more dolphins are more efficient at herding and maintaining the fish school as a tightly clustered unit against the water surface. As an alternative explanation, it might be assumed that the small groups stopped feeding after brief periods because individuals were satiated. In a larger group, with perhaps more individuals per fish school size and more competition, this would presumably take longer. Since small schools which fed briefly were, however, seen to feed more and more as the day advanced, it seems unlikely that they had fed to satiation previously. Therefore, either larger fish schools simply attract more dolphins, or it is of direct advantage to animals to feed in larger groups, and a mechanism for telling nearby groups that herding of foodfish is in progress may have evolved. Various investigators have reported seasonal variations in group sizes, but none appear to link such variations to a particular feeding mode as in the present study. Gaskin (1972) stated that dusky dolphins off New Zealand are found in smaller schools in winter and larger ones in summer, basically the same as in our study. New Zealand dusky dolphins feed on small squid and on surface fish, but it is not clear whether their relative dependence on these prey changes seasonally.

How do other groups know about the feeding bout 0.5-1.0 km distant? It is unlikely that at that

distance animals are actively echolocating on the fish school, and thus some behavior of the feeding dolphins is implicated. Perhaps underwater vocalizations serve as cues. The possibility of different sound emissions by dolphins feeding and not feeding has not yet been investigated in the present study, although Tyack (1976) found such a variation in wild bottlenose dolphins. The incidence of noisy—omnidirectional sound source—leaps increases before and during feeding, and these may provide cues to nearby dolphins. Norris and Dohl (1980) discussed the likelihood of leap sounds serving a communication function. We believe that the likelihood of such a function specifically in dusky dolphin feeding is great. If noisy leaps serve to attract or inform nearby schoolmates, and are at least in part designed to do so, this recruitment behavior may be analogous to the "drumming" recruitment of African chimpanzees, described by Reynolds and Reynolds (1965) and others. Saayman and Tayler (1979) suggested that recruitment may occur in *Sousa* sp. off South Africa as well, but they did not link it to the possibility of aerial behavior in their population.

How do groups orient towards feeding locations from a distance of more than several kilometers? Our underwater recordings of sounds created by leaps suggests that they probably do not propagate much over 1 km. Norris and Dohl (1980) also found rapid attenuation for underwater Hawaiian spinner dolphin leap sounds. But, we observed dolphins that were leaping towards a large feeding bout from as far as 8 km. One possible explanation is that at least one dolphin swam to the distant group with information about the feeding bout, a feat not unknown in the animal kingdom (von Frisch 1967, on honey bees). We have no evidence that such messenger service may take place, and suggest a possible alternative. (Although Eberhard and Evans 1962, Evans and Dreher 1962, and Dreher and Evans 1964 reported that individuals of the Pacific bottlenose dolphin, *Tursiops gilli,* have been seen detaching from a group, moving to "investigate" something, and then going back to the group. Their interpretation of scouting behavior, however, is open to speculation.) When we saw dolphins swimming towards a feeding bout from more than a few kilometers, we saw individuals leaping out of the water in high forward leaps, clearing the water by as much as three times their own length, and thus leaping as high as 4-5 m. This leaping became lower and finally subsided altogether as the animals came closer to the activity. It seems possible that dolphins are using in-air vision to orient to the feeding bout, taking the birds flying above the activity and the leaping dolphins of the activity as a cue. We present this as a tentative hypothesis because many investigators do not believe that dolphins have a high degree of long-range in-air visual acuity. Dral (1975), Herman et al. (1975), and Rivamonte (1976), however, believe that *Tursiops* sp. may have good in-air vision at infinity. Perhaps dolphins gain information about the feeding bout in some other manner, and are leaping that high and often simply as part of their rapid movement (although such high leaps are not seen during after-feeding rapid movement). The high leaps may decline when the dolphins get near the activity because they are tiring. If it should prove, however, that dolphins are capable of long-range vision, and use it in this manner, it would mean that the birds associated with dolphin feeding—up to now assumed to represent a parasitic or neutral role as they scavenge on the dolphins' herding efforts—may serve as a signal to other dolphins. Dolphin leaps would assume a similar in-air signaling function. To observers, the number of birds above an activity was a sign of the feeding activity's "success," and if dolphins can see these birds, there is no reason to assume that they could not as well gage such activity level.

Various different types of leaps and aerial displays are associated with different stages of surface feeding. What function could these leaps serve? To answer this question we will attempt to reconstruct a typical feeding bout in detail: Before surface feeding, dolphins move rapidly, and dive for long periods, indicating that they are covering a large distance and are looking for fish deeper than a few meters below the surface. Immediately before and during feeding, forward movement stops and long dives continue, interspersed with clean, noiseless leaps. During these leaps, animals reenter the water headfirst and rapidly swim down. We therefore believe that the clean leaps allow dolphins to breathe rapidly, and then forcefully and efficiently return to the depths. The humping variant of this leaping type appears similar to the headfirst surface dive employed by experienced skin divers.

As long dives decrease, a tightly bunched fish school, usually numbering several thousand fish in an area 3-5 m in diameter, is first seen at the surface. It thus appears that dolphins actively herd fish towards the surface, probably to use the

surface as a wall through which the prey cannot escape. This function has also been suggested by Norris and Dohl (in press), and shown to be carried out by some large predatory fishes by Major (1976; cited by Norris and Dohl in press).

Noisy leaps, which started at some point before the fish school appeared, continue throughout surface feeding. We gained the subjective impression that these leaps occurred on the periphery of feeding bouts. This may be because breaching directly into the fish school would certainly not be of advantage in keeping it tight against the water surface. As well, it may serve to keep fish from escaping, and thus may be an acoustic or vibration "netting" effect. We often saw dolphins tailslapping rapidly (2-3 slaps/s) while moving in a tight circle around feeding bouts, and this action may further serve to keep fish from escaping (it has been described by Norris and Dohl (1980) and labeled "motorboating").

Besides the function of recruiting nearby groups to the feeding bout either purposefully or incidental to keeping fish from escaping, there is a third possibility. The splashes of noisy leaps create an underwater omnidirectional sound which may actually serve to frighten fish and cause them to school more tightly. Although work has been done on schooling relative to pressure waves (Bobbi Low[6]) as far as we know, no studies exist on sounds and fright reactions in schooling fish.

While the feeding bout continues, clean leaps and humpings continue as well, and dolphins still dive steeply. They also come up at a sharp angle, and individuals move rapidly through the bunched fish school, appearing at the other side of the school with several fish in their mouths. They then dive steeply again, and usually resume "attacks" on the fish school from below. The dolphins may stay below the fish much of the time to keep the school from escaping downward, and possibly to herd other fish to the surface to continue or prolong feeding. This is not the first indication of apparent cooperative herding and feeding in dolphins. It appears that many different species cooperate in herding, and it has been described for representatives of the genera *Orcinus, Tursiops, Sousa, Phocoena, Delphinus,* and others (see Norris and Dohl in press). Many terrestrial predators do so as well (Wilson 1975).

[6]Bobbi Low, professor, University of Michigan, Ann Arbor, MI 48109, pers. commun. 1976.

Acrobatic noisy leaps are most often seen during and after feeding. These may herd fish and recruit nearby groups, but they appear to require much energy and coordination which seems unnecessary just to make noise. We believe with Norris and Dohl (1980) that they may serve a "social facilitation" function, signaling a high activity level as individuals reaffirm and strengthen social and possibly sexual bonds. Saayman and Tayler (1973, 1979) describe similar high activity levels in *Sousa* sp. when two or more groups meet, and provide a similar assessment. We suggest that individual animals have taken care of the basic requirement of feeding and are now prepared to spend time socializing and "playing."

After feeding, dusky dolphins are more willing to associate with boats, human swimmers, whales, sea lions, and inanimate objects such as kelp. This may be an outgrowth of the high level of social activity at that time. Although we also saw much apparent mating after feeding, we were not able to compare it with amount of mating in small, nonsurface-feeding groups.

When many small groups coalesced to form a large one, did the smaller units remain intact or was movement of dolphins throughout the large group "random"? We saw individuals which had been spaghetti-tagged in a small group traveling together within a feeding bout a few days after tagging (Würsig in press), and thus have some indication that the small group remained intact. This agrees with data by Norris and Dohl (1980) on Hawaiian spinner dolphins. They found that there is fluidity in schools, but that small groups of 4-10 animals may be the only units with longer term continuity. We have no long-term information on group stability. However, studies of other dolphins suggest that the small-unit group composition is constantly changing (Saayman and Tayler in press, humpback dolphins; Shane 1977; Würsig 1978; Wells et al. in press, bottlenose dolphins). This flexibility in small-group composition at least superficially resembles chimpanzee group structure, and Saayman and Tayler (1979) and one of us (Würsig 1978) independently speculated that the similarity comes from feeding on unpredictable and patchy food distribution (see also Nishida 1968). If a similar group structure is found in dusky dolphins, it might be possible that individuals move randomly throughout the large after-feeding group, and that the entire group of up to 300 animals forms the more stable breeding unit or population.

Captured animals were of both sexes (Würsig in press). As well, there were usually only 1 or 2 calves or small young within a group of about 15 animals, suggesting that mating is not highly polygynous. Given data from captivity (Evans and Bastian 1969 and Caldwell and Caldwell 1972 provided reviews) suggesting that promiscuity is a prominent feature of most odontocete cetaceans at least in unnatural circumstances, it is likely that the dusky dolphin social system is promiscuous as well. However, Bateson (1974) suggested rather stable relationships between some spotted, *Stenella attenuata,* and spinner dolphins for play, mating, and sleep.

We found that young were born mainly in the austral summer. If we assume an 11-12 mo gestation period (Sergeant et al. 1973 for bottlenose dolphins), most effective matings took place outside the winter season. If sexual activity continues throughout the year, then we can assume that there is a physiological change in males or females that allows conception to peak during the spring or summer. Seasonal changes in testis weight have been found for several cetacean species (for example, Ridgway and Green 1967 for *Delphinus delphis* and *Lagenorhynchus obliquidens*). It is possible that a similar physiological change may exist in dusky dolphins. This might relegate some activity appearing to serve a sexual function to the role of greeting or bond-strengthening ceremonies as has been suggested by Caldwell and Caldwell (1967), Bateson (1974), and others. We suspect, but have no definitive proof, that most mating occurs in large groups after surface feeding. Since this feeding occurs mainly in spring and summer, it correlates well with the summer calving peak. Nevertheless, if this is so, it would not invalidate the possibility of a seasonal physiological cycle, nor of "mating" at times serving a purely social function.

Groups which had about 10-20 adults and as many calves occurred at times. We saw these nursery groups mainly at the periphery of large feeding activities. They did not appear to participate in the high-activity level characteristic of large feeding bouts and after-feeding. Perhaps, when small groups feed, females with young feed and then split off as activity increases. This can be of adaptive value. Young may in this way avoid possible aggression and competition within the large feeding aggregation, and they may avoid possible predation by killer whales and sharks attracted to the activity. We saw large (3-5 m) unidentified sharks moving in dolphin feeding activity on four separate occasions, but they did not appear to bother the adult dolphins engaged in feeding.

The relationship of dusky dolphins and bottlenose dolphins was in some ways puzzling. Dusky dolphins moved in generally deeper water than bottlenose dolphins, but the two at times probably came into acoustic range of each other. Yet they did not appear to take notice of each other, although both species independently sought contact with southern right whales, sea lions, and the boat. Dusky dolphins were found in shallow water in the morning, but bottlenose dolphins were in even shallower water in the morning, then moved into intermediately deep water around noon, then into shallow water once again. It has been suggested (Würsig and Würsig 1979) that bottlenose dolphins may have been feeding on southern anchovy, the same food as that of dusky dolphins in these intermediate waters. At any rate, by that time of day, dusky dolphins were more often found in deeper water, and as a result, their food niches did not appear to overlap. As well, the two species were found with approximately opposite frequency within sight of the study area at different times of year. This suggests that one or both species may at times have actively avoided the other, although alternative explanations such as different ecological requirements may be more important.

Bottlenose dolphins moved in small groups close to shore, dusky dolphins moved in small groups while not feeding, but in larger groups around feeding time. Bottlenose dolphins appeared to spend most of their nearshore time feeding individually or perhaps in groups of two and three on large solitary fishes inhabiting nearshore rocks. Large groups are possibly not of advantage in exploiting a presumably scattered food resource. On the other hand, dusky dolphins appeared to hunt in small groups spread out over a large area, thus increasing their food-finding efficiency for a patchily distributed food resource. When food was found, they rapidly coalesced, and appeared to herd prey cooperatively, allowing more efficient feeding.

Dusky dolphins fed near the surface in deeper water in the afternoon, and moved slowly and with little activity in early morning. We suggested that the surface-feeding pattern may be associated with availability of fish at different times of day and in different areas of water. A similar change in area from nonfeeding to feeding was found for

Hawaiian spinner dolphins (Norris and Dohl 1980) and for *Sousa* sp. (Saayman and Tayler 1979). But what about the consistently shallow-water movement in the morning (and all day in winter) when dolphins did not appear to be surface feeding much of the time? Their activity level was low and they did not move rapidly. They ignored or avoided boats as well as other marine mammals. They moved in small, tight groups and we therefore gained the subjective impression that they were schooling in an almost "fishlike" manner. Because level of activity was low, objects in their paths were avoided or ignored, and schooling was tight, we believe that the dolphins were resting at this time.

There is some evidence that killer whales may prey on dusky dolphins. On three occasions when killer whales came close to dolphin groups, the dolphins moved into extremely shallow water. At the same time, they moved rapidly along shore, perhaps to avoid nearshore predation, of which killer whales are known to be capable on more stationary prey, such as elephant seals and sea lions (Norris and Prescott 1961; Tomilin 1967; pers. obs.). As well, their nearshore movement may serve to hide them from possible *Orcinus orca* echolocation, which might be confused and inefficient in very shallow water.

These observations make it likely that nearshore movement while resting is a defense against predation. In shallow water, killer whales (and possibly deepwater sharks) cannot come from below, nor from the flanking shoreline. When danger comes from the open sea, dolphins can retreat to very shallow waters in which larger predators cannot maneuver as efficiently. Norris and Dohl (1980) postulated a similar function for nearshore resting of Hawaiian spinner dolphins, suggesting that these animals possibly avoid large deepwater sharks during morning periods of low activity. Saayman and Tayler (1979) also saw *Sousa* sp. very close to shore when killer whales were near, and suggested that the dolphins might avoid predation in a similar manner. In the present population, it is possible that nearshore movement during low-activity levels may serve other functions as well, but we believe that the predator-avoidance hypothesis may be at least part of the reason.

CONCLUSION

In the preceding discussion, we attempted to link observed behavior patterns to observed or possible ecological variables. We recognize that this endeavor is highly incomplete, and that many more alternative explanations will be made available in the future. One important factor that may have been somewhat obscured in the results and discussion of behavior should be emphasized. Dolphin behavior in captivity as well as in the wild appears highly plastic and variable. For example, dusky dolphins feed on southern anchovy. Yet many species are more catholic feeders (for example, Gunter 1942, Leatherwood 1975, for *Tursiops truncatus;* and Perrin et al. 1973, for *Stenella* spp.), and it is certain that dusky dolphins engage in other feeding than surface feeding described here. We hope that future work will shed light on other feeding modes, whether subsurface feeding is done cooperatively as is surface feeding, or whether it is performed more often by single dolphins on nonaggregated prey. Such an analysis may help us understand the dramatic difference in movement patterns and general activity levels between times when dolphins feed cooperatively on the surface and when they feed in other ways.

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GROWTH AND SURVIVAL IN NEWLY SETTLED SPAT OF THE MANILA CLAM, *TAPES JAPONICA*

JOHN G. WILLIAMS[1]

ABSTRACT

Substrate abundances of adult Manila clam, *Tapes japonica*, were manipulated in July 1976 on a portion of beach dug commercially in the southern region of Puget Sound, Washington. Differences in clam spat growth and survival were measured between samples taken from substrates having varying levels of adult clam abundance.

The clam spat settled at 0.206 mm long. Initial growth of clams settling in the fall was much slower than for clams settling in the summer, 9 months versus 2 months, respectively, to reach approximately 2.5 mm long. Summer settling clams form a visible growth checkmark by October of their first year at approximately 5-8 mm. Fall settling clams form their first visible checkmark during their second October at approximately 14-16 mm. The length of clams was found to be significantly less for clams growing in substrates with natural or high adult clam abundances versus those from substrates with no adult clams.

Only 1.2% of the initial population of clams that settled in September 1976 survived until June 1977. The most likely cause of this mortality was by meiofaunal predators, particularly nematodes. By June, no difference in survival rates was detectable between clams from substrates that contained no adult clams versus those from substrates with natural or high adult clam abundance.

Clam spat movement occurred along the beach and may have contributed to the high spat mortality.

The Japanese little-neck or Manila clam, *Tapes japonica* Deshayes, is a native to Japanese and Korean waters, but was introduced into Puget Sound, Wash., along with the Pacific oyster, *Crassostrea gigas*, in the 1930's (Quayle 1964). It has since become an important part of the commercial Puget Sound hard-shell clam fishery with approximately 1 million lb harvested annually. It has also been so heavily utilized by the sport fishery that the populations on some Puget Sound beaches have been almost eliminated.

The majority of research on the Manila clam has been performed in Japan (see Tamura 1966 for a review of the Japanese literature). Because the water temperatures and climate in Puget Sound are cooler than those in most of the Japanese study areas, the results published by the Japanese with respect to spawning times, growth, and population numbers can be misleading when applied to clam populations in this area. Studies conducted on the west coast of the United States and Canada dealt with gonad development (Holland and Chew 1974), planktonic larval stages (Quayle and Bourne 1972), and growth and/or survival after settling and after some arbitrary body size, usually based on sieve retention, had been reached (Jones 1974; Glock 1978; Lukas[2]). Nosho and Chew (1972) made the only attempt to investigate early settling stages of the Manila clam. However, due to the sieve size they used, they were unable to detect newly settled spat. The lack of early life history information is probably related to the difficulty in sorting out newly settled spat from gravel samples, and in specific indentification. Loosanoff et al. (1966) found it difficult to identify pelagic larvae to species and cited this as a reason for incomplete life histories of many pelecypods. Quayle (1952) found that identification of spat was even more difficult than the identification of planktonic larvae.

I began a study in the summer of 1976 to describe the growth and survival of Manila clams from settling size to formation of the first growth ring. In addition, since the study was located in an area with large numbers of adult Manila clams, I investigated the possibility that the pres-

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[2]Lucas, G. 1973. Clam-abalone spawning and rearing. Commer. Fish. Res. Dev. Act. July 1, 1970 to June 30, 1973. Fish. Comm. Oreg. Proc. Rep., 19 p.

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ence of adults may influence or be associated with spat growth and survival.

METHODS

In 1976 a study site was chosen in southern Puget Sound on a narrow estuary called Little Skookum Inlet (Figure 1). The site was on intertidal land from which Manila clams were commercially harvested. There was easy access to the beach, but because of its private ownership, the probability of people tampering with the experimental plots was low.

Plot Construction

To study the possible influence of adult clams on the growth and survival of spat, I constructed plots in which I experimentally manipulated the beach material to yield different concentrations of adult clams. Each plot contained four treatments, as follows:

Treatment 1. No adult clams and new substrate. All beach material was removed to a depth of 15 cm to ensure removal of adult clams. Gravel from the high intertidal (+3 m) was then carried down to fill the excavated hole to the existing beach level.

Treatment 2. No adult clams and old substrate. All beach material was removed to a depth of 15 cm and then sifted through a 12 mm mesh screen to remove the adult clams. All screened material and any large rocks retained on the screen were then returned to the excavated hole and enough additional screened material was added from residue of Treatment 1 to bring the treatment level to the same height as the beach.

Treatment 3. Moderate adult clam density (control). A shovel blade was inserted vertically, 15 cm into the substrate on the edge of the treatment. The handle was pulled back and forth 3 or 4 times until the surface above the blade was loosened. The shovel blade was inserted and agitated around the perimeter of the treatment until the entire surface area of the plot had been disturbed. No clams were added to or subtracted from the treatment, and no counts of naturally occurring clams in the treatment were made prior to the settling experiments.

Treatment 4. High adult clam density. This treatment was disturbed in the same manner as

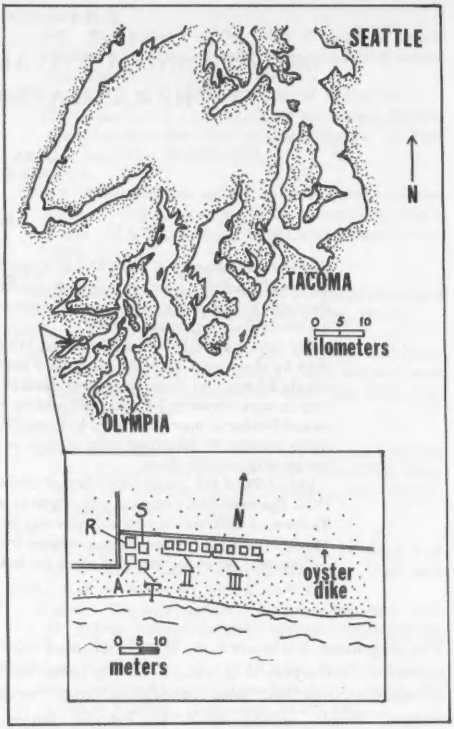

FIGURE 1.—Diagrammatic representation of the study site for the Manila clam on Little Skookum Inlet in southern Puget Sound, Wash., on a minus tide (MLLW). Plots A, II, and III were established in July 1976. Plots R, S, and T were established in July 1977. Plots A, R, S, and T were 2 × 2 m squares divided into 16 sections each and Plots II and III each contained four 1.5 × 1.5 m sections in a row.

Treatment 3. In addition, enough adult clams between 2.0 and 5.0 cm in length were placed on the surface of the treatment to create a surface density of approximately 480/m². This density was the number of clams necessary to completely cover the surface area.

In all cases, the day following the construction of Treatment 4, no clams remained on the beach surface, and a large number of new siphon holes were apparent. In no case were any adult clams found in Treatments 1 or 2, and it was thus assumed that the clams added to Treatment 4 buried within the treatment and did not move to adjacent treatments or outside the plot. I as-

sumed that any predation on the clams before they were able to bury within the substrate did not substantially affect the magnitude of the adult clam density, as compared with the other treatments.

I constructed Plots A, II, and III in July 1976, and Plots R, S, and T in July 1977 at a tidal height ranging from +0.25 m to +0.75 m (MLLW datum), as determined by the height of the nearby oyster dikes (Figure 1). For Plots A, R, S, and T, wooden lath stakes were driven into the ground to delineate 2 × 2 m squares, that were then subdivided by stakes into four rows and four columns. The result was sixteen 0.25 m^2 subareas in each plot. Four replicates of Treatments 1-4 were then constructed within each plot to form a 4 × 4 Latin square array of treatments. For Plots II and III, stakes were driven into the ground to delineate a 1.5 m wide by 12.0 m long plot. Treatments 1-4 were randomly assigned to subareas within the plot so that the resulting configuration consisted of four different 1.5 × 1.5 m treatments, separated by 1.5 m spaces between each treatment, within each plot.

A continuously recording thermograph was buried 1 cm below the surface gravel next to Plot A in October 1976. The recording tape was replaced monthly.

The large plots were constructed to minimize possible edge effects caused by the close proximity of treatments to each other. To further minimize possible edge effects, samples were taken only from the inside 0.25 m^2 area of each treatment in both the large and small plots.

Sampling

To check for newly settled clams, each week I took two or three gravel samples beside each plot by twisting a 20.28 cm^2 clear plastic tube 2 cm deep into the beach. A small hand trowel was then shoved down beside and rotated under the tube as it was removed from the gravel, preventing any material from falling out. The contents of the tube were then transferred to a bottle or plastic bag. A 10% formaldehyde solution with a concentration of 0.01% phloxine B dye was then added to the container.

In the laboratory, I washed the gravel samples through a series of Tyler[3] sieves. Sieving down to mesh size of 0.149 mm was necessary to insure retainment of the smallest, newly settled spat in freshly preserved samples. The residue from the finest sieve was placed in a Petri dish under a compound dissecting scope (50×) and examined for clam spat.

In 1976, when a large larval settlement was detected from the weekly gravel samples, I sampled all of the treatment areas in each plot. I constructed a sampling template from a piece of 1.91 cm thick plywood that had the inside 0.125 m^2 removed. Seine twine was stretched over the opening to form a 5 × 5 grid with each square 5.72 cm on a side.

For each individual treatment area in a plot, five squares in the grid were randomly selected as the sample sites from which to take cores. After removing the cores, the holes were filled to beach level with gravel taken from beside the plot, at a depth of 4 cm, in order to avoid introducing newly settled spat to the plots.

To follow the growth and survival from settling size, I took 10 cores per treatment in November and December 1976 and in January, March, and April 1977 from Plots A and II. The location of the cores within each treatment was randomly selected, excluding all core areas previously utilized. In June 1977 the remaining core areas in the different treatments were sampled. For each sampling period, all cores in each treatment were sieved in the laboratory, the clams were counted, and a height and length measurement was taken on the first 30 clams encountered per treatment.

Sample Sizes

Twenty core samples per treatment were taken immediately after newly settled clams were observed. Using methods given by Elliott (1971), I determined that the number of clam spat per core per treatment had a negative binomial distribution. The counts were transformed ($\log_{10} X$) and a mean and variance computed. These numbers were utilized in Elliott's formula for the determination of sample sizes. A standard error equal to 20% of the mean and a 95% confidence were used. The results showed that a sample size of 5 for each treatment would have been sufficient. Based on this and the amount of time necessary to process each core, 10 cores per treatment were chosen as the sample size for subsequent sampling periods.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

Summer Sampling in 1977

To follow the growth of the 1976 fall settlement for 1 yr, three random 0.25 m², 3 cm deep gravel samples were taken from near Plot A in early August 1977, and again in the middle of September. No treatment effect determinations were possible due to a lack of sufficient study plots. Material was preserved by freezing, instead of by a formaldehyde solution. In the laboratory the material was thawed and washed through Tyler sieves (1.190 mm minimum mesh size), and then the residue on the screens was placed in a large cake pan. The clams were sorted by eye, and a height and length measurement was taken on all clams.

Core samples taken from Plots R, S, and T, in the summer and fall of 1977 to test for larval settlement were used as the basis for determining the growth of the clam spat that settled in July 1977.

RESULTS

Growth

To test for possible changes in the height-length ratio due to growth, a linear regression was run on $\log_{10}$-transformed height versus length measurements for clams from settling size through 1 yr. Correlation was high (r = 0.997) and thus only length measurements were used to express results. A plot of clam lengths determined from samples taken after the initial settlement in September 1976 through the following 12 mo is shown in Figure 2.

The average length of newly settled clams was 0.206 mm (N = 129; SE = 0.01). The clam spat that settled in September 1976 grew about 2.5 times their settling length in 2 mo. Little growth occurred between November and January; growth commenced again by the middle of March. By June the spat had attained a length of 2.17-2.7 mm.

In contrast to the growth of the fall settlement, the clams that settled in July 1977 attained an average length of 2.82 mm (N = 47; SE = 0.12) by the middle of September. This was a growth of 13.5 times their size at settling in 2 mo and was slightly larger than the size reached in 9 mo by clams from the fall settlement.

Growth rings were laid down in October. Clams that settled in July attained an average length of

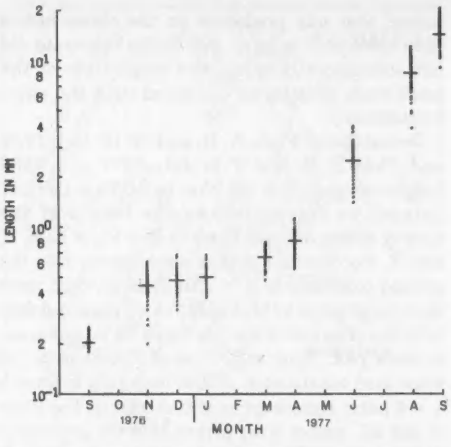

FIGURE 2.—Plot of individual and mean length measurements of Manila clams recovered during sampling periods. Sample sizes from September 1976 to September 1977 were 129, 136, 97, 72, 67, 94, 61, and 110.

6.16 mm (N = 42; SE = 0.51) by this time. Clams that settled in the fall also formed rings their first October, but since they were so small, the mark was not discernable by the following summer. By September 1977 the clams from the fall settlement had attained an average length of 14.93 mm (N = 110; SE = 0.26). Approximately 0.5 mm growth occurred before the end of October, at which point their first growth ring was visible. Clams that settled in July were about 23 mm long 1 yr later.

No differential growth was detectable until June 1977 between clams that settled in fall 1976 into the different experimental treatment substrates. A Kruskal-Wallis rank sums test on clams sampled in June detected a significant difference (P<0.001) between those sampled from substrates with no adult clams and those from substrates with adult clams. The treatments were ranked by the average length of clams that each contained (Treatment 2 had the largest clams; Treatment 3 had the smallest). A series of one-tailed Mann-Whitney pairwise comparisons (pairwise P<0.05) were performed to test which treatments differed significantly (Hollander and Wolfe 1973). The following were the results (no significant difference between pairs underlined in common):

<u>2 1</u> <u>4 3</u>

Clams from substrates with no adults (Treatments 1, 2) averaged 2.70 mm (N = 55; SE = 0.08) long, and clams from substrates with moderate (Treatment 3) and high (Treatment 4) adult clam abundances averaged 2.17 mm (N = 39; SE = 0.08).

Survival

The density of newly settled clams sampled from 105 cores ranged from 19 to 93, with a mean of 54.3. Only 1.2% of the clams (equivalent to 250-450/m²) survived until June 1977, 9 mo after the fall 1976 settlement (Figure 3). The largest loss in clams occurred during the first 2 mo after settling when the density decreased by 57%. During the third, fourth and next 2 (combined) mo after settling, the average density decrease from the previous sampling period was 34%, 56%, and 35%, respectively. A Kruskal-Wallis test on the June data detected no differential (P>0.50) survivorship between clams that had settled into substrates with adult clams versus those that settled into substrates with no adult clams.

DISCUSSION

Growth

There has been a great disparity in the reported size of 1-yr-old Manila clams. Three areas in Japan have reported three different lengths: in Hokkaido, 8 mm (Yamamoto and Iwata 1956); in the Inland Sea, 18 mm (Ohba 1959); and in Ariake Bay (South Japan), 27 mm (Tanaka 1954). Rodde et al. (1976) grew Manila clams to 34 mm in 1 yr under hatchery conditions with high temperatures and nutrient rich water. Nosho and Chew (1972) estimated that Manila clams in Hood Canal, Wash., were 24 mm at the end of 1 yr. These conflicting reports have created some difficulties for scientists in attempting to determine the age of Manila clams found in Puget Sound beaches. The fact that I found two sizes of clams that resulted from settlements only a few months apart makes this understandable. In some cases, others have based growth data on checks in the shell without studying the early stages of growth. However, without the knowledge about the time of year that a clam cohort settled and the period of growth until the formation of the first visible checkmark, the determination of the age of a clam can be difficult.

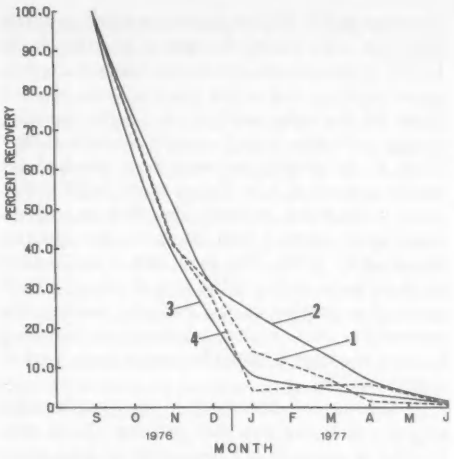

FIGURE 3.—Survival of Manila clams at each sampling period for Treatments 1-4 expressed as a percentage of the initial levels at settlement.

The results of my research showed that growth rings were formed by the end of October. For clams that settled in the summer the first visible check was formed at 3-4 mo, but for those settling in the fall (just 2-3 mo later), the first visible mark was formed in 13 mo. The modal lengths, that I found until the first visible checkmark was formed, of 5-8 mm and 14-16 mm for the summer and fall cohorts should give scientists a more concise baseline upon which to judge growth data for the Manila clam.

Although there was a difference in the growth rates between clams that settled in the summer and those that settled in the fall, the length of newly settled clams that I observed was the same for both periods and the same as those found by Loosanoff et al. (1966) at the Milford Laboratory in Connecticut and by Yoshida (1953) in Japan. The clams from the fall settlement more than doubled in size in 2 mo, but then their growth almost ceased for a 3 mo period and slowly increased until March. This slow winter growth was very similar to Japanese findings on larger Manila clams (Yoshida 1935; Yamamoto and Iwata 1956; Ikematsu 1957; Ohba 1959). In southern Puget Sound, Glock (1978) found no growth during this same period for Manila clams with lengths from 12 to 20 mm. Wilbur and Owen (1964) stated that growth is generally negligible for most molluscan species below 5°-10° C, which

corresponded to the temperatures found in Little Skookum Inlet during the winter months (Table 1). The growth for the summer settling clams was much higher, and other studies with Manila clams of the same settling size have reported similar or higher initial growth. Yoshida (1953) found clams settling in early June reached 0.9 mm by the end of July. Clams raised in 22°-29° C water under hatchery conditions, with an optimal food supply, were 5 mm 90 days after settling (Rodde et al. 1976). The small size at settlement for the Manila clam and the slow initial growth of clams that settled in the fall underscores the necessity to use a small mesh size when sampling for spat so as not to possibly mask a large part of their early life.

In addition to a difference in the growth rates between summer and fall settling clams, the lengths of clams that I recovered in June were significantly greater ($P<0.001$) in treatments without adult clams than in treatments with adult clams. A similar decreased growth with increased densities has also been shown for larger Manila clams in other studies. Sagara (1952) found this for clams >30 mm, but indicated that clams <20 mm were not affected by density. Ohba (1956) found decreased growth in 10-12 mm clams and related it to competition for food. In other studies, Hancock (1973) found reduced growth with *Cardium edule* in areas of overpopulation and a marked reduction in size in locally overcrowded areas. Finally, in a hatchery-rearing experiment with 14 mm Manila clams, Langton et al. (1977) found that growth increased with ration size in crowded conditions. A decrease in available food to juveniles was implicated as the controlling factor that caused the decrease in clam growth observed in treatments with adult clams, as compared with those in treatments without adults. There were not sufficient study plots available to determine whether this differential growth continued during the summer. The results of these experiments indicates that the harvest of adult clams from a beach will allow for a better growth of undersized clams. This result coincides with the general view of commercial Manila clam harvesters in Puget Sound (Taylor[4]).

TABLE 1.—The daily average and the extreme substrate temperatures (1 cm below surface) between sampling periods for the Manila clam in Little Skookum Inlet, Wash., at the +0.6 m tide level.

Sampling period	N	Temperatures (° C)	
		Average	Extremes
1976:			
Oct. 24-Nov. 20	30	11.6	10.5-12.5
Nov. 20-Dec. 20	30	9.7	6.5-10.5
Dec. 20-Jan. 16, 1977	27	7.8	4.0- 9.0
1977:			
Jan. 16-Feb. 2	17	8.6	3.0- 9.0
Mar. 11-Apr. 8	28	9.5	5.5-20.0
Apr. 8-May 6	28	12.2	11.0-18.5
May 6-June 4	29	12.8	12.0-20.0
June 4-July 4	30	15.6	14.5-28.0
July 4-6	3	16.7	16.5-21.5
July 30-Aug. 4	6	17.8	16.5-19.0
Aug. 25-Sept. 21	27	16.7	15.5-23.0
Sept. 21-Oct. 12	21	15.6	10.0-16.5

Survival

Approximately 1.2% of the clams that settled in September 1976 survived until June 1977. Japanese studies on Manila clams have reported similar low levels of survivorship 4-9 mo after initial settlements. Ikematsu (1957) found that spat densities of 5,000/m² in March were only 1.0% of the 500,000/m² he found the previous November. Ohba (1959) estimated settling densities of 25,000/m² in October, but found only 8.0% of that (2,000/m²) by the following June. In studies on a number of clam species other than Manila clams, Muus (1973) reported that regardless of clam densities at settling, the number of clams recovered per unit area decreased rapidly until a density of several hundred per square meter was approached. The level of survivorship from the fall settlement was similar to these studies but although it was low, the number of spat that it represented (250-450/m²) was more than 2.5 times greater than the density of adults (approximately 100/m²) considered as an adequate level at which a beach can be dug commercially (Taylor see footnote 4).

Not only was the survivorship from the fall settlement low, but the majority of the clam spat mortality occurred during the first 2 mo after settling (57%) and only about 10% of the clams survived to 0.7 mm long (6 mo). One or more of a number of factors are usually identified as causes of high mortality in biological populations. In the case of benthic marine invertebrates, Hancock (1970) stated that survival after settlement will depend upon: a) environmental conditions, notably temperature; b) food supply, which may be affected by intra- and interspecific competition; c) space competition; d) parasites and disease; e) ac-

[4]Justin Taylor, Totten Seafood, Route 1, Box 372A, Olympia, WA 98502, pers. commun. June 1977.

cidental ingestion of newly settled young (of some molluscs by adults of the same or different species; f) physical damage or disturbance; and g) predation. Most of the above factors did not appear to be significant in this study.

a) Yoshida (1953) experimented with 1.0-3.8 mm Manila clams and found a survival of 90% or greater in water temperatures averaging 7° C. The water temperatures at Little Skookum averaged 8.9°-12.7° C during winter and probably were an insignificant cause of mortality, except during the coldest part of January (Table 1). Low water temperature probably attributed to the slight increase in clam spat mortality observed at this time.

b) When Cahn (1951) surveyed the Japanese Manila clam fishery, he cited starvation under overcrowded conditions of newly settled spat as a probable cause of death. The survival rate in this study, however, remained fairly equal between treatments with no adult clams and those with high adult clam densities. Thus, the expected cropping of the food supply to spat that settled among the adults did not appear to affect the spat's survival. In addition, almost nothing is known about the food requirements of newly settled spat, so adequacy of food supply as a controlling factor would be difficult to determine.

c) Lack of sufficient space for growth between two consecutive year classes was proposed by Hancock (1973) as one of the largest factors controlling survival of newly settled spat in *C. edule*. He proposed that space requirements for growth of shells would conflict in two adjacent year classes, with the smaller cockles being forced from the substrate as they grew. In nonadjacent year classes, 0-group cockles could maintain their position between shells of older adult clams. This hypothesis was based on clams first observed when 10 mm long. Space limitation did affect survival of the spat in this study, because their size was quite small compared with the space available for growth.

d) There was no evidence of parasites and/or disease in either the adult stocks or the newly settled spat.

e) Under experimental conditions, Kristensen (1957) found that inhalation by adult cockles of newly settled spat could cause death of the small spat, even when the larvae were discharged soon afterward. Hancock (1973), however, did not feel that the presence of adults adversely affected survival of settled young in his studies at Burry Inlet, but he felt that mortalities were related to oyster catcher, *Haematopus ostralegus*, predation. Since he did not look at the spat until 5 mo after they had settled, it would be difficult to determine at which stage in their early life history the largest mortality occurred. In the present study, the largest initial settlement occurred in Treatment 1, but by April this treatment had not only the lowest survival but also the lowest absolute density of the four treatments. If mortality was caused by ingestion by adults, then a higher density would have been expected for Treatment 1, which contained no adults.

f) Shellbourne (1957) studied small oysters and found that shifting surface sands subjected newly settled spat and juveniles to increased mortality due to abrasion. Quayle (1952) felt the largest cause of mortality for the spat of *Venerupis pullastra* was the unsuitability of the substrate. Glock (1978) planted small (2-4 mm) hatchery-reared Manila clams on a southern Puget Sound beach and then covered some of the area with protective mesh covering. He had a much higher survival rate under the areas with plastic mesh, and attributed this in part to stabilization of the sediment. He also found predation rates to be low. In this study, the Treatment 1 areas in Plots A, II, and III were readily observable through the third month after settling, due to a slight difference in color of the gravel brought down from the high intertidal area. This observation indicated that any movement of the surface gravel must have been slight in order not to mask the visible differences of this treatment. In the laboratory, I subjected the spat to considerable mechanical agitation during the process of washing and sieving; however, only a few of the thousands of spat that I observed had damaged shells. I also found some unbroken, empty clam shells that were equal in size to live clams sampled, but never a number of shells equivalent to the mortality observed. I concluded that abrasion did not cause substantial mortalities in this study.

g) Thorson (1966) felt that the biological factor with the greatest effect on survival of newly settled larvae was predation. Muus (1973) came to the conclusion after a very complete study on the early life history of newly settled bivalves in Denmark. Since the largest mortality in this study occurred when the spat were quite small, it seemed most probable that if predation were the cause, then the majority of the loss would be to

meiofaunal predators (defined as organisms that are retained on sieves 0.04-0.1 mm and passed through sieves 0.5-1.0 mm (McIntyre 1969; Coull 1973)), that were nearly the same size. Swedmark (1964) listed turbellarians, coelenterates, and nematodes as interstitial predators. Thorson (1966) cited studies that have shown turbellarians, nematodes, and harpacticoid copepods to be predators on newly settled spat. Although only a few turbellarians and no coelenterates were recovered during the study period, a large number of nematodes and harpacticoids were included in each core sampled. In spite of the citation by Thorson, the harpacticoids in this study were not likely to have eaten even the smallest clam spat, as these particular species are considered almost exclusively detritus feeders (Sibert et al. 1977; Illg[5]). The degree to which nematodes may have accounted for loss in clam spat is unknown. Although larger predators (shore crabs, drilling snails, sea stars, fish, birds) may account for significant predation losses on larger clams, their effect on survival of the newly settled spat was probably low. Large, active predators would not likely have expended the energy to forage for the small spat that would have provided little energy in return.

Of all the above factors listed, I concluded the major cause for the large loss in spat that I observed was due to predation by meiofaunal predators. Since some empty clam shells were found on the beach and vigorous sieving in the laboratory did not damage the shells of the spat, only predation could have accounted for both the high mortalities and the destruction or removal of shells. I assumed that nematodes were the dominant predator.

Movement of Clams on the Beach

Two experiments were performed (November 1976 and May 1977) to test for movement of small clams on the beach. In each case, 2 cm of surface gravel was removed from a plot that was 0.25 m^2, to insure that no small clams remained. One month after the start of each experiment, core samples were taken and small clams were found in the center of each plot that had been previously clam free. It was not known whether this movement was active or passive. Active movement implies that clams physically moved (probably by foot action) across the beach. Passive movement implies physical transport of clams across the substrate, with or without movement of surface gravel. In the present study, byssus threads were detectable on clams as small as 0.45 mm long. This indicated that they had the ability to attach to the substrate which would decrease their susceptibility to movement by currents. To the contrary, Sigurdsson et al. (1976) proposed that some postplanktonic bivalve larvae use their byssus threads as a method for dispersal. The method of transport would be analogous to the gossamer flight by young spiders. Either of these two methods for utilization of byssus threads may have been used by some of the calm spat at the study site.

Baggerman (1953), with *C. edule,* found that transportation of clams over the substrate may have been an important factor in the final distribution of clams. In this study, transportation may have played an important part in the growth and survival of the spat. Growth was shown to be significantly greater in treatments without adult clams than in treatments with adult clams. The adults thus may have directly caused a decrease in growth of juveniles by decreasing the availability of food, and/or indirectly they may have influenced clam spat to actively seek new substrates in which to resettle to avoid competition. Additionally, in the process of resettlement, clam spat may have become susceptible to a larger number of predators.

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[5]Paul Illg, Department of Zoology, University of Washington, Seattle, WA 98195, pers. commun. February 1977.

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DEVELOPMENT AND OCCURRENCE OF LARVAE AND JUVENILES OF THE ROCKFISHES *SEBASTES FLAVIDUS* AND *SEBASTES MELANOPS* (SCORPAENIDAE) OFF OREGON[1]

WAYNE A. LAROCHE AND SALLY L. RICHARDSON[2]

ABSTRACT

Developmental series of larvae and juveniles of two important and very similar species of northeast Pacific rockfishes (Scorpaenidae: *Sebastes*) are described and illustrated: *S. flavidus* (10.1-105.0 mm standard length) and *S. melanops* (10.6-111.6 mm standard length). Descriptions include a literature review, identification, distinguishing features, general development, morphology, fin development, spination, scale formation, pigmentation, and color of fresh specimens. The main differences between *S. flavidus* and *S. melanops* within the size range described are pectoral fin ray number (usually 18 versus 19), lateral line pore number (usually >50 versus <50), and caudal peduncle depth/caudal peduncle length ratio (mean values 0.73, 0.64, 0.64, 0.80 versus 0.88, 0.78, 0.74, 0.92 in postflexion larvae, transforming, pelagic juvenile, and benthic juvenile specimens, respectively). Occurrence of these two species in waters off Oregon is discussed. Small benthic juveniles of *S. flavidus* seem to inhabit deeper waters, >20 m depth, than those of *S. melanops*.

Comparisons are made among known larvae and juveniles of *Sebastes* species. Identification problems within the *S. flavidus-S. melanops/S. entomelas-S. mystinus* groups are discussed.

Rockfishes, *Sebastes* spp., represent an important commercial and recreational resource along the west coast of North America. In 1976, landings of rockfishes (all species) were 14,000 t, constituting 24% of the total trawl catch by the United States and Canada, second only to Pacific cod landings (Pacific Marine Fisheries Commission[3]). Since the decline of Pacific ocean perch, *S. alutus*, landings in the late 1960's, more rockfish species have been subjected to increasing fishing pressure (Verhoeven 1976). This situation, together with concern over managing the resource, has emphasized the need to determine the condition of rockfish stocks particularly in order to avoid overexploitation (Gunderson[4]). Knowledge of the early life stages, especially pelagic juveniles, is important since they provide valuable tools for resource assessment, systematics, evolution, and other emerging research areas.

This paper contributes new information on the early life history of two important rockfish species: yellowtail rockfish, *S. flavidus*, and black rockfish, *S. melanops*. They were among the five principal species in the Oregon trawl landings of "other rockfish" from 1963 to 1971, contributing 33 and 12% of the total landings during those 9 yr (Niska 1976). They are also important in the Oregon sport catch but landing data are not available.

Larval and juvenile development of these two species is described for the first time and occurrence of young off Oregon is discussed. Particular attention is given to problems involved with identification due to the extreme similarity of these two species as larvae and juveniles.

METHODS

Specimens described in this paper came from collections in the School of Oceanography, Oregon State University. The collections were obtained with 70 cm bongo nets, neuston nets, meter nets, Isaacs-Kidd midwater trawls, beam trawls, otter trawls, beach seines, and dip nets off the Oregon coast and in Oregon tidepools and estuaries since 1961. Samples were taken during all months of the

[1]From a final report for NOAA NMFS Contract No. 03-7-208-35263 submitted 15 September 1978 to NMFS Northwest and Alaska Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98112.

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[3]Pacific Marine Fisheries Commission. 1978. Data series. Bottom or trawl fish section. Pac. Mar. Fish. Comm., Portland, Oreg., p. 1-472, 500-509.

[4]Gunderson, D. 1976. Proceedings of the 1st rockfish survey workshop. Processed rep., 14 p. Northwest Fisheries Center, NMFS, NOAA, 2725 Montlake Boulevard East, Seattle, Wash.

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year and along the entire Oregon coast, but were concentrated along an east-west transect off Newport, Oreg. (lat. 44°39.1′ N). All specimens were preserved in 5 or 10% Formalin[5] and transferred to ≈40% isopropyl alcohol.

Our approach to identification, methods of making counts and measurements, and terminology for development and spination follow Richardson and Laroche (1979). Body parts measured include:

Standard length (SL) = snout tip to notochord tip preceding development of caudal fin, then to posterior margin of hypural plate.

Snout to anus length = distance along body midline from snout tip to vertical through posterior margin of hindgut at anus.

Head length (HL) = snout tip to cleithrum until no longer visible, then to posteriormost margin of opercle.

Snout length = snout tip to anterior margin of orbit of left eye.

Upper jaw length = snout tip to posterior margin of maxillary.

Eye diameter = greatest diameter of left orbit.

Interorbital distance = distance between dorsal margins of orbits.

Body depth at pectoral fin base = vertical distance from dorsal to ventral body margin at base of pectoral fin.

Body depth at anus = vertical distance from dorsal to ventral body margin immediately posterior to anus.

Caudal peduncle depth = shortest vertical distance between dorsal and ventral margins of caudal peduncle.

Caudal peduncle length = horizontal distance from base of posteriormost dorsal ray to posterior margin of hypural elements.

Pectoral fin length = distance from base to tip of longest ray.

Pectoral fin base depth = width of base of pectoral fin.

Pelvic spine length = distance from base to tip of pelvic spine.

Pelvic fin length = distance from base to tip of longest ray.

Snout to origin of pelvic fin = distance along body midline to vertical through insertion of pelvic fin.

Parietal spine length = distance along posterior margin of parietal spine from insertion to tip.

Nuchal spine length = distance along posterior margin of nuchal spine from insertion to tip.

Preopercular spine length (third spine; posterior series) = distance from tip to basal insertion if visible, or to a line connecting the points of deepest indentation between preopercular spines 2 and 3 and spines 3 and 4 (posterior series).

Length of angle gill raker = distance from tip of gill raker to point of articulation with gill arch.

Longest dorsal fin spine = distance from base to tip.

Longest dorsal fin ray = distance from base to tip.

Longest anal fin spine = distance from base to tip.

All body lengths given refer to standard length unless noted otherwise.

When the two posteriormost dorsal and anal fin rays arise from the same pterygiophore, they are counted as one.

A modified descriptive approach is used to minimize repetition which would result due to the extreme similarity in the development of *S. flavidus* and *S. melanops*. Descriptions are combined for both species and differences are noted as they occur. Reference to tabularized development morphology data, including relative body proportions and fin and head spine development, is made wherever practical to condense the description.

SEBASTES FLAVIDUS (AYRES) AND *SEBASTES MELANOPS* GIRARD (Figures 1-6)

Literature.—Pigment patterns of preextrusion larvae of *S. flavidus* were described by Delacy et al. (1964), including a figure, Westrheim (1975), and Moser et al. (1977). Preextrusion larvae (mean total length = 4.5 mm) have a row of usually <16 melanophores ($\bar{x}$ = 10, range 8-12 on 20 specimens) along the ventral body midline which stops short of the anus by at least four myomeres. The gut is pigmented and melanophore(s) are usually present on the ventral body surface near the notochord tip.

Larvae and juveniles of *S. melanops* have not been described.

Identification (Tables 1-3; Appendix Table 1).—Fifty-one specimens of *S. flavidus* (10.1-105.0 mm)

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

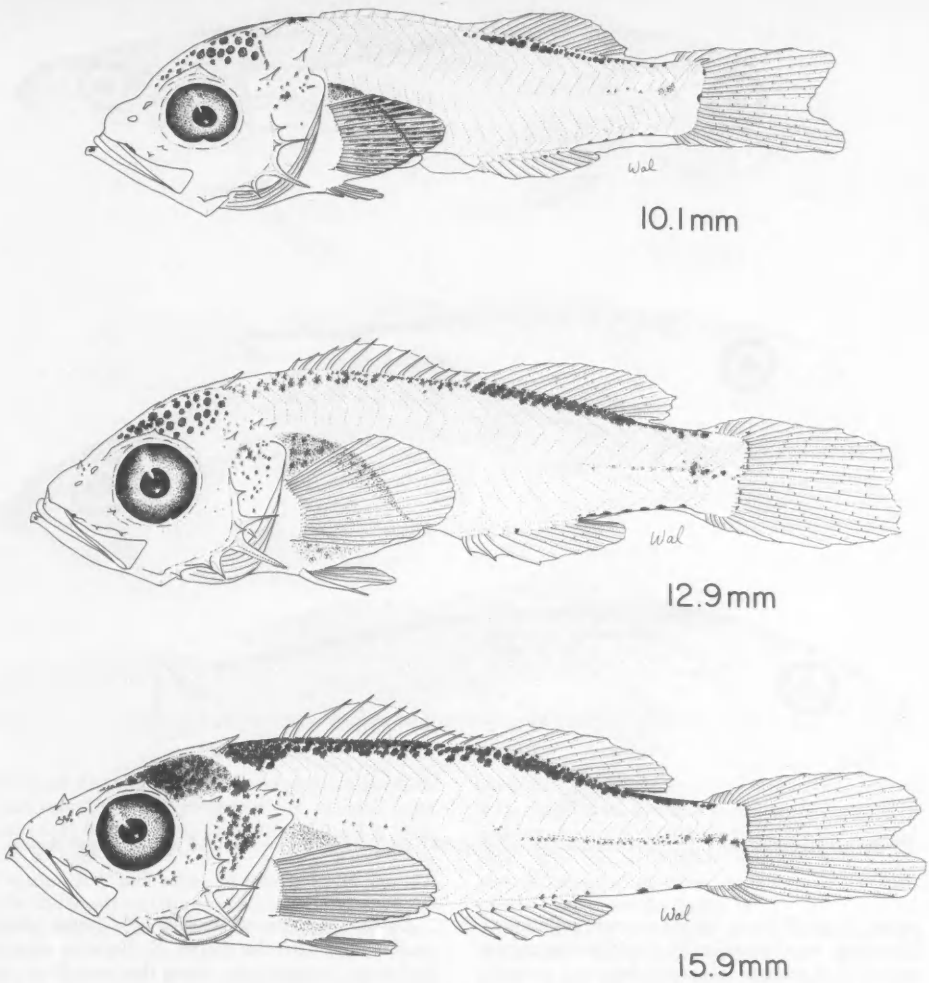

FIGURE 1.—Planktonic larvae (10.1, 12.9, 15.9 mm) of *Sebastes flavidus*.

were selected for the developmental series from 556 specimens identified. Juveniles were identified by the following combination of characters recorded from juvenile and adult specimens:

Gill rakers = 33-39
Lateral line pores = 46-57, usually 50-54
Pectoral fin rays = 17-19, usually 18
Anal fin soft rays = 7-9, usually 8
Dorsal fin soft rays = 14-15
Preocular spine = absent
Supraocular spine = absent
Interorbital space = flat to convex
Black blotch at base of spinous dorsal fin = present.

Fifty-eight specimens of *S. melanops* (10.6-111.6 mm) were selected for the developmental

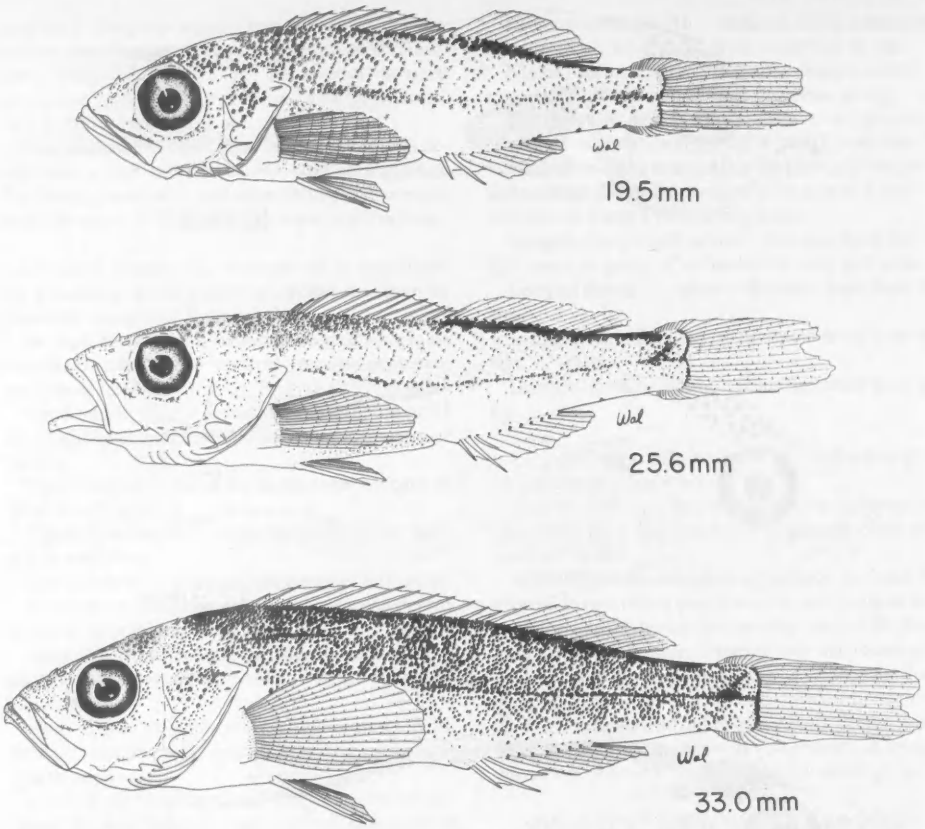

FIGURE 2.—Planktonic larva (19.5 mm), transforming specimen (25.6 mm), and pelagic juvenile (33.0 mm) of *Sebastes flavidus*.

series from 365 specimens in our collections. Juveniles were identified by the following combination of characters recorded from our juvenile and adult specimens:

Gill rakers	= 34-40
Lateral line pores	= 45-54, usually 47-50
Pectoral fin rays	= 18-20, usually 19
Anal fin soft rays	= 7-9, usually 8
Dorsal fin soft rays	= 14-16, usually 14-15
Preocular spine	= absent
Supraocular spine	= absent
Interorbital space	= flat to convex
Black blotch at base of spinous dorsal fin	= present.

Of the 36 *Sebastes* species off Oregon (Richardson and Laroche 1979), *S. flavidus* and *S. melanops*, respectively, have the best fit to the above characters. *Sebastes melanops* usually has 19 rather than 18 pectoral rays and a lower number (<50 rather than >50) of lateral line pores than *S. flavidus* based on counts made on juveniles and adults collected from Yaquina Bay, Oreg., and the Pacific Ocean nearby (Appendix Table 1). Juvenile specimens were identified by us as *S. flavidus* and *S. melanops* using the above characters together with color pattern (intensity of melanistic pigment on caudal fin) and location of capture (*S. flavidus* from depths >25 m and *S. melanops* from depths <15 m). Of 52 *S. flavidus*

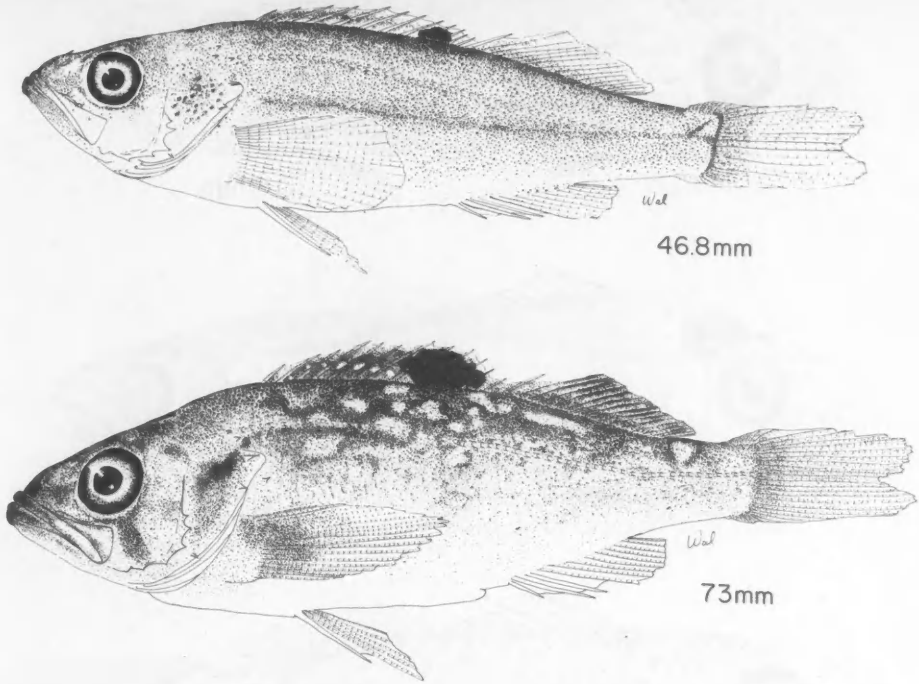

FIGURE 3.—Pelagic juvenile (46.8 mm) and benthic juvenile (73 mm) of *Sebastes flavidus*.

taken off Yaquina Bay (the area offshore of which most larval and pelagic juvenile *S. flavidus* were collected), 96% had a pectoral fin ray count of 18 on one or both sides. Of 66 *S. melanops* taken in Yaquina Bay and adjacent tidepool and shallow subtidal locations (the area offshore of which most larval and pelagic juvenile *S. melanops* were collected), 95% had a pectoral fin ray count of 19 on one or both sides. Mean numbers of lateral line pores were 52.33 ±0.52 (95% confidence) (N = 48) and 49.20 ±0.42 (95% confidence) (N = 66) on the left side of *S. flavidus* and *S. melanops*, respectively. No significant difference was found between counts made on the left and right sides for either species. Two specimens of *S. flavidus* had 19 pectoral fin rays on both sides but lateral line pores numbered >50 on both sides. Three specimens of *S. melanops* had 18 pectoral fin rays on both sides but lateral line pores numbered <51 on both sides. Thus the number of pectoral fin rays and lateral line pores allow positive identification of *S. flavidus* in most cases. Although diagonal scale rows below the lateral line were not used in making the initial identifications, they are useful when they can be counted and can help verify identifications when other characters are not conclusive (see Appendix Table 1).

Specimens of *S. flavidus* and *S. melanops* were selected for the developmental series only if pectoral fin ray counts on both sides were ≤18 and ≥19, respectively, to minimize possible confusion. The presence of discrete melanophores at the articulation of dorsal and anal fin soft rays and melanophores along the posterior margin of the hypural plate together with counts helped link the developmental series and distinguish the specimens from all other Oregon species. The more slender and longer caudal peduncle of *S. flavidus* and the deeper, shorter caudal peduncle of *S. melanops* (Table 2) helped tie each series together, confirm identifications, and eliminate confusion between the two species.

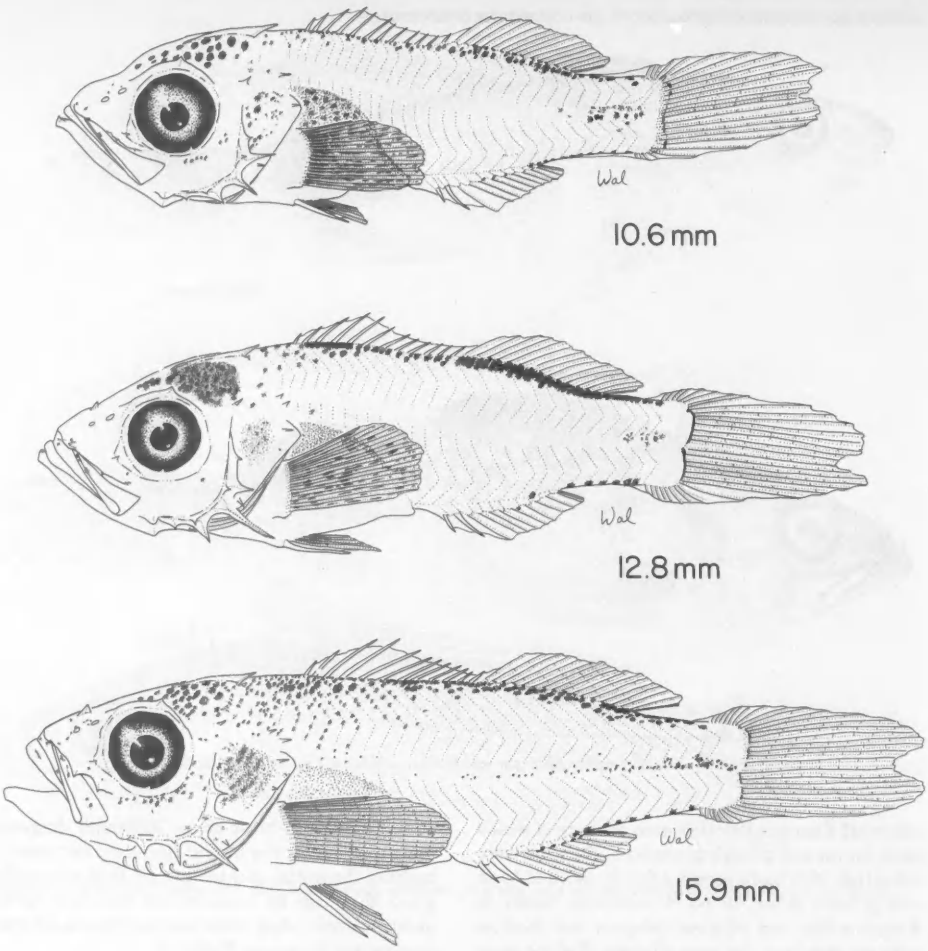

FIGURE 4.—Planktonic larvae (10.6, 12.8, 15.9 mm) of *Sebastes melanops*.

Distinguishing Features.—Characters useful to distinguish the smallest identified larvae (10-11 mm) of *S. flavidus* and *S. melanops* from those of other *Sebastes* species are the moderately pigmented pectoral and pelvic fins, presence of pigment along the dorsal body surface under the dorsal fin, internal and external melanophores above the notochord at and anterior to the point of notochord flexion, melanophores along the dorsal and ventral margins of the caudal peduncle, and melanophores at the articulation of some dorsal and anal rays. The relatively long and narrow caudal peduncle and presence of 18 pectoral rays distinguishes *S. flavidus*, and the relatively deep and short caudal peduncle and presence of 19 pectoral rays distinguish *S. melanops*. Meristics,[6] lack of preocular and supraocular spines, flat to

[6]The term "meristics" is used to refer to all countable characters which are usually arranged in series.

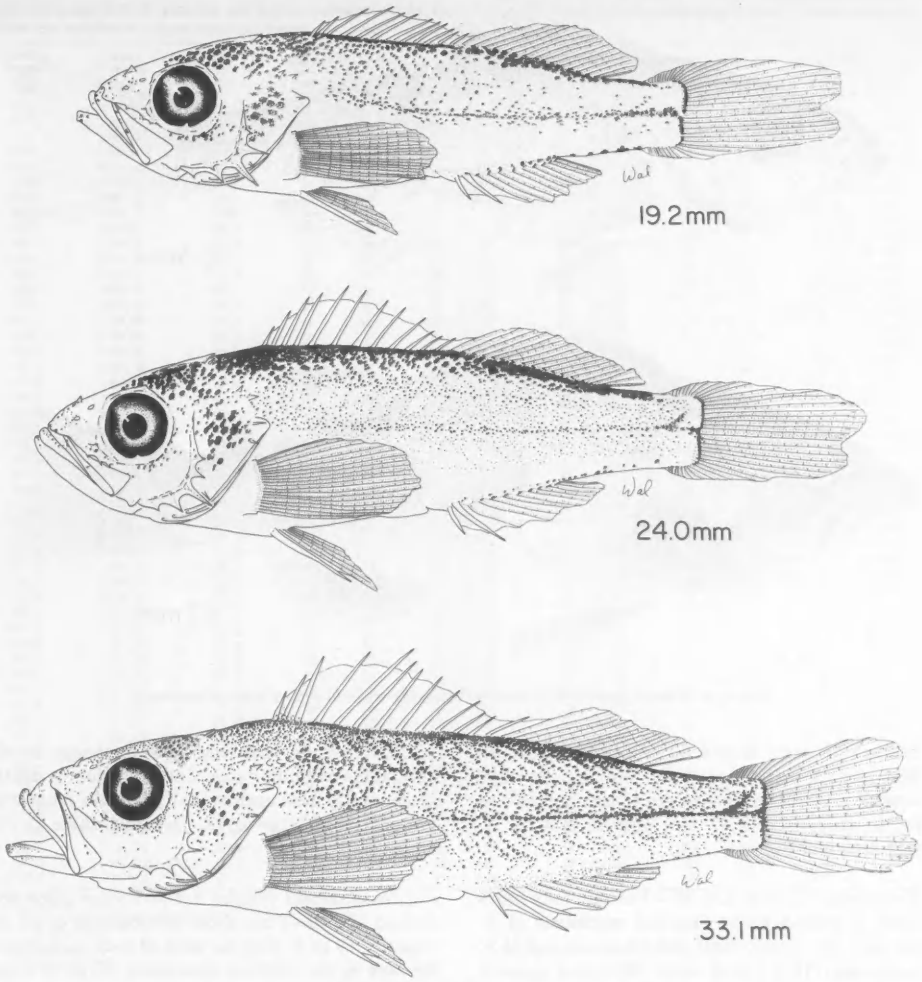

FIGURE 5.—Pelagic larvae (19.2, 24.0, 33.1 mm) of *Sebastes melanops*.

convex interorbital space, body and fin pigmentation, and body morphometry together serve to distinguish larger larvae and juveniles from those of other Oregon species.

General Development.—Notochord flexion is complete on the smallest larva of *S. flavidus* (10.1 mm) and *S. melanops* (10.6 mm) identified. Transformation from postflexion larvae to pelagic juveniles occurs between 23 and 27 mm in *S. flavidus* and between ≈24 and 33 mm in *S. melanops* as indicated by the structural change of the "prespines" in the dorsal and anal fins to sharp, hard spines. Melanistic pigmentation gradually increases over the body through the larval and transformation periods and shows no marked change during transformation. Transition from pelagic to benthic habitat usually occurs when

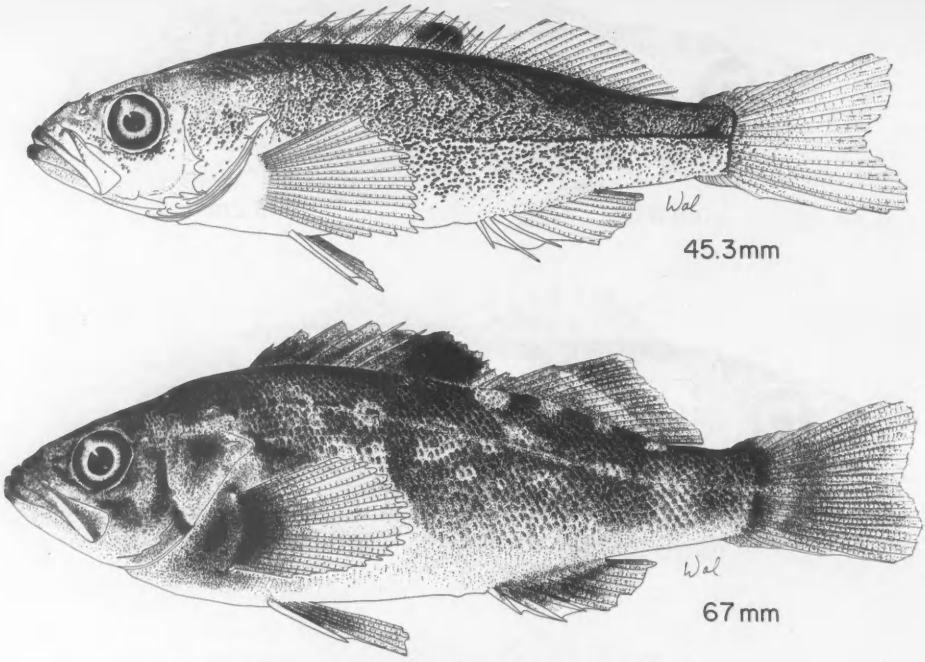

FIGURE 6.—Pelagic juvenile (45.3 mm) and benthic juvenile (67 mm) of *Sebastes melanops*.

fish are between 40 and 50 mm in both species. The largest pelagic juvenile and the smallest benthic juvenile observed were 45 mm and 42 mm for *S. flavidus* and 47 mm and 38 mm for *S. melanops* (see Figures 7-10).

Morphology (Tables 2, 4, 5).—Various body parts were measured on 51 selected specimens of *S. flavidus* (10.1-105.0 mm) and 58 specimens of *S. melanops* (10.6-111.6 mm). Relative growth trends are summarized in Table 2.

The most important morphometric character which will separate most *S. flavidus* from *S. melanops* is the caudal peduncle depth/length ratio. While the depth and length of the caudal peduncle change only slightly during development, their ratio changes notably. In *S. flavidus* it decreases from 73 to 64 or 65% in pelagic stages, increasing again to 80% in benthic juveniles. In *S. melanops* it decreases from 88 to 74-77% in pelagic stages and then increases to 89% in benthic juveniles. This ratio is usually smaller in *S. flavidus* than in *S. melanops* for all specimens of similar size. Caudal peduncle depth is generally less and caudal peduncle length is generally greater in *S. flavidus* than in *S. melanops*.

Fin Development (Tables 1-4).—Pectoral fins are formed and have the adult complement of 17-19 (usually 18 in *S. flavidus* and 19 in *S. melanops*) fin rays in the smallest specimens (10 or 11 mm) in the series. The fins in both species are moderate in length, reaching 24 or 25% SL in juveniles.

The adult pelvic fin complement (I, 5) is present by 10 or 11 mm in both species. The pelvic fins are of moderate length, averaging 13-18% SL during the pelagic period. Pelvic spine length is always less than pelvic fin length.

The adult complement of 8 + 7 principal caudal rays is present on the larvae of both species along with six superior and five inferior secondary caudal rays. Counts of superior and inferior secondary rays made on three stained juvenile *S.*

TABLE 1.—Meristics from larvae and juveniles of *Sebastes flavidus* off Oregon, based on unstained specimens. Counts of left and right pelvic fin rays (I,5;I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7;7) were constant from the smallest to largest specimen listed.

Standard length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
10.1	(1), 15	III[2],8	18	18	—	—	—	—	—	—
10.3	XIII[2],14	III[2],8	18	18	—	—	—	—	—	—
10.7	XIII[2],14	III[2],8	18	18	—	—	—	—	—	—
11.4	XIII[2],15	III[2],8	18	18	—	—	—	—	—	—
11.8	XIII[2],14	III[2],8	18	18	—	—	—	—	—	—
11.8	XIII[2],15	III[2],8	18	18	—	—	—	—	—	—
11.9	XIII[2],15	III[2],8	18	18	—	—	—	—	—	—
12.0	XIII[2],15	III[2],8	18	18	—	—	—	—	—	—
12.2	XIII[2],15	III[2],8	18	18	—	—	—	—	—	—
12.7	XIII[2],15	III[2],8	18	18	23+ 8=31	23+ 9=32	—	—	—	—
12.8	XIII[2],15	III[2],8	18	18	23+ 9=32	24+ 9=33	—	—	—	—
12.9	XIII[2],15	III[2],8	18	18	23+ 9=32	23+ 9=32	—	—	—	—
13.1	XIII[2],15	III[2],7	17	18	22+ 8=30	23+ 9=32	—	—	—	—
13.7	XIII[2],15	III[2],7	18	18	23+ 9=32	23+ 9=32	—	—	—	—
14.4	XIII[2],15	III[2],8	18	18	24+ 9=33	23+ 9=32	—	—	—	—
14.8	XIII[2],14	III[2],8	18	18	24+ 9=33	23+ 9=32	—	—	—	—
15.8	XIII[2],15	III[2],9	18	18	24+ 9=33	24+ 9=33	—	—	—	—
15.9	XIII[2],14	III[2],7	17	18	24+10=33	23+ 9=32	—	—	—	—
16.4	XIII[2],15	III[2],8	18	18	24+10=34	24+10=34	—	—	—	—
16.8	XIII[2],15	III[2],7	18	18	24+10=34	25+10=35	—	—	—	—
18.9	XIII[2],15	III[2],8	18	18	24+10=34	24+10=34	—	—	—	—
19.5	XIII[2],15	III[2],8	18	18	25+10=35	24+10=34	—	—	—	—
19.8	XIII[2],15	III[2],8	18	18	25+10=35	25+10=35	—	—	—	—
20.5	XIII[2],15	III[2],9	18	18	25+10=35	24+11=35	—	—	—	—
21.3	XIII[2],15	III[2],8	18	18	25+10=35	25+10=35	—	—	—	—
22.3	XIII[2],15	III[2],8	18	18	24+10=34	25+10=35	—	—	—	—
[3]23.6	XIII[2],15	III[2],8	18	18	25+11=36	26+10=36	—	—	—	—
[3]23.7	XIII[2],15	III ,8	18	18	25+11=36	26+11=37	—	—	—	—
[3]24.2	XIII[2],15	III ,8	18	18	26+11=37	26+11=37	—	—	—	—
[3]24.8	XIII[2],15	III[2],8	18	18	25+10=35	25+11=36	—	—	—	—
[3]25.6	XIII[2],15	III ,8	17	17	25+10=35	25+11=36	—	—	—	—
[3]26.6	XIV[2],15	III[2],8	18	18	24+10=34	24+10=34	—	—	—	—
[3]26.7	XIII[2],15	III ,8	18	18	27+10=37	26+11=37	—	—	—	—
[4]28.6	XIII ,15	III ,8	18	18	25+10=35	26+11=37	—	—	—	—
[4]29.2	XIII ,15	III ,8	18	18	26+10=36	26+10=36	—	—	—	—
[4]29.6	XIII ,15	III ,8	18	18	26+10=36	27+11=38	—	—	—	—
[4]30.4	XIII ,15	III ,8	18	18	25+11=36	26+11=37	—	—	—	—
[4]33.0	XIII ,14	III ,8	18	18	26+11=37	27+11=38	—	—	—	—
[4]33.1	XIII ,15	III ,8	18	18	25+10=35	25+10=35	—	—	—	—
[4]35.2	XIII ,14	III ,8	18	18	26+11=37	26+11=37	—	—	—	—
[4]36.4	XIII ,14	III ,8	18	18	26+11=37	27+11=38	—	—	—	—
[4]37.6	XIII ,15	III ,8	18	18	25+11=36	25+10=35	—	—	—	—
[4]41.9	XIII ,15	III ,8	18	18	28+11=39	28+11=39	—	—	—	—
[4]43.6	XIII ,15	III ,8	18	18	25+10=35	25+11=36	—	—	—	—
[4]45.2	XIII ,15	III ,8	18	18	27+11=38	28+11=39	—	—	—	—
[5]67.6	XIII ,14	III ,8	18	18	26+11=37	26+11=37	54	54	56	56
[5]71.5	XIII ,15	III ,8	18	18	27+11=38	26+11=37	48	53	—	55
[5]72.5	XIII ,14	III ,8	18	18	26+11=37	27+10=37	52	53	54	54
[5]77.5	XIII ,14	III ,8	18	18	26+11=37	25+10=35	50	53	55	56
[5]81.0	XIII ,14	III ,7	18	18	26+11=37	26+11=37	52	53	—	—
[5]105.0	XIII ,14	III ,8	18	18	27+11=38	26+11=37	55	56	57	—

[1]Forming.
[2]Posteriormost dorsal and anal spine appears as a soft ray.
[3]Transforming.
[4]Pelagic juvenile.
[5]Benthic juvenile.

flavidus (49, 50, and 52 mm long) were 12/13, 12/13, and 12/12, respectively. Counts on four stained juvenile *S. melanops* (42, 43, 47, and 48 mm long) were 12/13, 12/12, 12/12, and 12/13, respectively. Adult complements of the dorsal and anal fin spines and rays can be counted by ≈11 or 12 mm. The transition of the 13th dorsal and 3d anal fin "prespines" to spines is complete by ≈27 mm in *S. flavidus* and ≈33 mm in *S. melanops*.

Spination (Tables 2, 4-7).—Spines present on the left side of the head of the smallest (10.1 mm) larval *S. flavidus* include the parietal; first, second, third, and fourth posterior preopercular; first and third anterior preopercular; postocular; pterotic; superior opercular; first inferior infraorbital; first superior infraorbital; inferior posttemporal; and the developing interopercular (indicated by a small blunt projection). The smallest

TABLE 2.—Body proportions of larvae and juveniles of *Sebastes flavidus* and *S. melanops*. Values given are percent of standard length (SL) or head length (HL) including mean, standard deviation, and range in parentheses. Number of specimens measured may be derived from measurements listed by developmental stage (as indicated by footnotes) in Tables 4 and 5.

Item	*Sebastes flavidus*	*Sebastes melanops*
Body depth at pectoral fin base/SL:		
Postflexion	28.2±1.72(25.3-30.8)	29.6±1.77(26.3-32.8)
Transforming	24.5±0.62(23.6-25.6)	26.1±0.79(25.2-27.5)
Pelagic juvenile	24.8±1.08(23.3-26.9)	25.9±0.72(24.7-26.7)
Benthic juvenile	30.0±1.00(28.4-31.0)	30.9±1.94(27.0-33.0)
Body depth at anus/SL:		
Postflexion	22.3±1.01(20.6-24.2)	24.3±1.24(21.8-26.1)
Transforming	20.0±0.51(19.2-20.7)	21.9±0.89(20.9-23.3)
Pelagic juvenile	21.3±0.99(19.9-23.4)	22.2±0.71(20.9-23.6)
Benthic juvenile	25.6±1.11(23.5-26.3)	26.4±0.75(25.3-27.4)
Snout to anus length/SL:		
Postflexion	57.3±1.77(53.5-61.2)	58.0±2.15(54.0-62.2)
Transforming	60.0±1.23(57.5-60.5)	58.9±3.02(55.8-62.6)
Pelagic juvenile	60.3±1.02(58.8-62.3)	61.3±1.65(59.4-65.3)
Benthic juvenile	63.2±1.22(62.2-65.6)	63.0±3.43(59.4-70.7)
Snout to pelvic fin origin/SL:		
Postflexion	37.9±1.86(34.4-42.7)	38.8±1.86(35.8-42.9)
Transforming	35.9±0.49(35.3-36.7)	37.3±1.94(34.8-39.3)
Pelagic juvenile	36.2±0.73(35.3-37.7)	36.8±1.63(35.2-40.1)
Benthic juvenile	39.7±2.37(37.2-43.0)	38.2±2.38(35.4-41.8)
Head length/SL:		
Postflexion	38.6±1.78(35.4-42.7)	38.5±1.95(34.8-42.9)
Transforming	35.0±0.91(33.7-36.0)	35.0±2.19(31.9-37.8)
Pelagic juvenile	33.4±1.34(31.9-36.0)	33.3±1.45(31.1-35.3)
Benthic juvenile	35.2±2.52(33.4-40.0)	34.8±1.83(32.3-37.3)
Eye diameter/HL:		
Postflexion	32.0±2.06(27.1-35.4)	30.8±1.61(26.9-34.1)
Transforming	28.9±0.72(27.8-29.8)	28.6±1.90(26.0-30.6)
Pelagic juvenile	27.2±1.29(25.7-29.1)	26.3±1.49(24.0-28.9)
Benthic juvenile	26.8±1.78(24.1-29.5)	25.6±1.70(23.4-28.7)
Upper jaw length/HL:		
Postflexion	42.6±1.84(39.0-45.9)	42.1±2.21(37.3-45.7)
Transforming	40.5±2.35(37.5-44.0)	41.2±2.02(37.6-42.7)
Pelagic juvenile	42.1±1.33(39.2-44.4)	41.4±1.71(39.3-44.2)
Benthic juvenile	42.5±2.89(39.3-46.5)	44.2±4.16(35.3-48.4)
Snout length/HL:		
Postflexion	27.4±1.74(23.9-30.8)	27.6±1.65(25.0-31.4)
Transforming	26.3±0.38(25.6-26.7)	26.7±1.13(25.8-28.0)
Pelagic juvenile	25.6±1.75(23.1-29.1)	27.0±2.12(23.9-30.0)
Benthic juvenile	28.8±3.56(22.9-32.7)	23.1±1.98(19.9-26.5)
Interorbital distance/HL:		
Postflexion	28.8±1.78(25.0-31.9)	29.0±2.11(24.0-32.7)
Transforming	24.8±0.71(24.1-26.2)	25.9±1.01(24.7-27.0)
Pelagic juvenile	24.7±1.67(21.6-28.0)	24.2±1.25(22.2-26.2)
Benthic juvenile	22.2±0.98(21.4-24.1)	23.6±1.97(21.1-26.2)
Angle gill raker length/HL:		
Postflexion	12.1±1.46(9.0-14.5)	10.9±1.36(7.3-13.5)
Transforming	14.7±0.84(13.9-16.1)	12.2±1.92(10.6-15.0)
Pelagic juvenile	14.4±1.13(11.7-16.2)	14.1±1.04(13.1-16.1)
Benthic juvenile	15.0±0.66(14.4-16.1)	14.9±0.71(14.1-15.8)
Longest dorsal spine length[1]/HL:		
Postflexion	19.4±6.84(5.0-32.4)	24.0±5.11(15.2-31.9)
Transforming	32.8±1.53(31.0-34.5)	—
Pelagic juvenile	35.3±1.68(33.7-39.3)	36.9±2.46(33.3-39.5)
Benthic juvenile	34.6±1.81(31.7-36.7)	35.4±1.35(33.9-37.8)
Longest dorsal ray length[2]/HL:		
Postflexion	30.5±4.39(19.0-38.1)	32.6±3.70(25.0-38.3)
Transforming	36.7±1.59(35.2-39.3)	36.9±3.07(34.9-40.4)
Pelagic juvenile	40.5±3.00(37.1-45.8)	40.1±1.62(38.5-43.0)
Benthic juvenile	43.4±2.34(40.3-46.1)	46.1±2.34(45.2-48.5)
Longest anal spine length[3]/HL:		
Postflexion	16.5±4.96(10.8-26.3)	19.2±3.99(11.3-25.6)
Transforming	26.2±2.25(22.2-28.7)	30.4±2.95(27.1-32.7)
Pelagic juvenile	30.6±2.41(26.2-33.6)	32.3±2.44(28.7-37.7)
Benthic juvenile	33.8±1.36(31.9-35.4)	34.7±1.97(31.2-37.1)
Pectoral fin length/SL:		
Postflexion	20.1±1.91(15.8-22.7)	21.7±1.41(18.5-24.5)
Transforming	22.5±1.01(21.4-24.3)	24.0±1.08(22.8-25.5)
Pelagic juvenile	24.6±0.35(24.1-25.1)	24.2±0.90(22.4-25.2)
Benthic juvenile	24.1±1.30(21.8-25.7)	24.7±1.57(22.9-27.2)
Pectoral fin base depth/SL:		
Postflexion	8.5±0.90(7.2-10.9)	8.8±0.69(7.7-10.1)
Transforming	7.0±0.22(6.7-7.3)	7.7±0.18(7.5-7.9)
Pelagic juvenile	7.0±0.45(6.1-7.6)	7.8±0.12(7.6-8.0)
Benthic juvenile	8.4±0.34(7.8-8.7)	9.4±0.39(8.5-9.8)
Pelvic fin length/SL:		
Postflexion	13.4±1.83(8.9-16.7)	15.4±1.17(12.6-17.4)
Transforming	15.5±0.59(14.6-16.1)	16.4±0.30(16.1-16.7)
Pelagic juvenile	16.3±0.89(14.8-17.8)	17.5±0.64(16.8-18.8)
Benthic juvenile	19.5±0.51(19.0-20.4)	20.7±1.44(18.2-23.0)
Pelvic spine length/SL:		
Postflexion	10.4±2.46(6.3-15.7)	12.6±1.57(9.2-14.9)
Transforming	13.7±0.92(12.7-15.3)	11.4±0.92(10.8-12.1)
Pelagic juvenile	13.6±0.88(12.6-15.4)	14.0±0.56(12.8-14.5)
Benthic juvenile	12.1±0.72(11.3-13.2)	13.3±2.04(10.7-13.9)
Parietal spine length/HL:		
Postflexion	8.8±2.17(4.2-11.8)	7.9±2.00(4.2-11.4)
Transforming	4.0±0.67(3.4-4.7)	5.6±0.35(5.3-5.8)
Pelagic juvenile	1.0±0.45(0.7-1.7)	1.2±0.64(0.7-1.6)
Benthic juvenile	—	—
Nuchal spine length/HL:		
Postflexion	2.1±1.15(0.1-3.9)	1.6±0.87(0.4-3.2)
Transforming	2.1±0.31(1.8-2.6)	2.6±0.35(2.4-2.9)
Pelagic juvenile	1.9±0.72(1.1-2.4)	1.4±0.24(1.2-1.7)
Benthic juvenile	—	—
Preopercular spine length/HL:		
Postflexion	20.1±3.30(12.8-27.0)	19.5±3.31(14.5-26.9)
Transforming	12.8±2.16(10.0-16.0)	13.3±1.11(11.8-14.4)
Pelagic juvenile	10.2±1.60(7.8-13.0)	9.6±0.81(8.4-10.9)
Benthic juvenile	3.2±0.86(2.4-4.8)	2.3±1.15(0.4-4.5)
Caudal peduncle depth/SL:		
Postflexion	11.3±0.71(10.0-12.6)	12.8±0.89(11.4-14.3)
Transforming	9.7±0.43(9.0-10.2)	11.1±0.54(10.5-11.7)
Pelagic juvenile	9.7±0.29(9.3-10.4)	10.3±0.27(9.7-10.5)
Benthic juvenile	10.5±0.38(9.9-11.0)	11.3±0.23(11.0-11.6)
Caudal peduncle length/SL:		
Postflexion	15.5±0.89(13.4-16.8)	14.6±0.70(13.0-16.2)
Transforming	15.1±0.54(14.3-15.7)	14.3±0.17(14.2-14.6)
Pelagic juvenile	15.1±1.06(14.1-17.8)	13.9±0.66(12.8-14.9)
Benthic juvenile	13.2±0.88(12.0-14.5)	12.6±0.69(11.6-13.4)
Caudal peduncle depth/caudal peduncle length:		
Postflexion	.73±0.060(0.65-0.83)	.88±0.069(0.74-1.06)
Transforming	.64±0.029(0.60-0.69)	.78±0.042(0.73-0.84)
Pelagic juvenile	.64±0.046(0.56-0.74)	.74±0.034(0.70-0.81)
Benthic juvenile	.80±0.072(0.70-0.90)	.92±0.021(0.91-0.94)

[1]Usually fourth or fifth in larvae, fifth or sixth in juveniles.
[2]Usually in anterior one-fourth of fin.
[3]The second spine in larvae and transforming larvae, the third spine in juveniles.

S. melanops (10.6 mm) has a nuchal and supracleithral (as blunt bumps) and a fourth superior infraorbital in addition to the spines listed above.

In both species the parietal spine and ridge are finely serrated on all specimens <34 mm long. Parietal spine length decreases with development becoming overgrown in benthic juveniles. The nuchal spine, always shorter than the parietal, is usually present in larvae and pelagic juveniles and is overgrown by scales and tissue in benthic juveniles. (Table 2 lists the mean nuchal spine/HL value for pelagic juveniles as greater than the

TABLE 3.—Meristics from larvae and juveniles of *Sebastes melanops* off Oregon, based on unstained specimens. Counts of left and right pelvic fin rays (I,5;I,5), superior and inferior principal caudal rays (8,7), and left and right branchiostegal rays (7;7) were constant from the smallest to the largest specimen listed.

Standard Length (mm)	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays		Gill rakers (first arch)		Lateral line pores		Diagonal scale rows	
			Left	Right	Left	Right	Left	Right	Left	Right
10.6	XIII[1],15	III[1],8	19	19	—	—				
11.7	XIII[1],15	III[1],9	19	19	—	—				
11.9	XIII[1],15	III[1],8	19	19	—	23+ 8=31	—	—	—	—
11.9	XIII[1],15	III[1],8	19	19	21+ 8=29	21+ 8=29	—	—	—	—
12.4	XIII[1],15	III[1],8	19	19	22+ 9=31	24+ 8=32	—	—	—	—
12.8	XIII[1],14	III[1],8	19	19	23+ 9=32	22+ 8=30	—	—	—	—
12.8	XIII[1],15	III[1],8	19	19	23+ 8=31	23+ 8=31	—	—	—	—
12.8	XIII[1],14	III[1],8	19	19	21+ 8=29	22+ 9=31	—	—	—	—
13.5	XIII[1],15	III[1],8	19	19	23+ 9=32	23+ 9=32	—	—	—	—
13.6	XIII[1],14	III[1],8	19	19	22+ 8=30	23+ 9=32	—	—	—	—
13.9	XIII[1],15	III[1],8	19	19	22+10=32	22+ 9=31	—	—	—	—
14.0	XIII[1],15	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
14.9	XIII[1],14	III[1],8	19	19	23+ 9=32	22+ 8=30	—	—	—	—
15.4	XIII[1],13	III[1],8	19	19	21+ 9=30	23+ 9=32	—	—	—	—
15.4	XIII[1],15	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
15.7	XIII[1],15	III[1],8	19	19	24+ 9=33	24+ 9=33	—	—	—	—
15.9	XIII[1],15	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
16.4	XIII[1],14	III[1],8	19	19	23+ 9=32	23+10=33	—	—	—	—
16.5	XIII[1],15	III[1],8	19	19	23+10=33	23+ 9=32	—	—	—	—
17.2	XIII[1],14	III[1],8	19	19	24+ 9=33	23+10=33	—	—	—	—
17.4	XIII[1],15	III[1],8	19	19	25+10=35	25+10=35	—	—	—	—
17.4	XIII[1],14	III[1],8	19	19	23+10=33	23+ 9=32	—	—	—	—
17.7	XIII[1],15	III[1],8	19	19	24+ 9=33	24+10=34	—	—	—	—
17.7	XIII[1],15	III[1],8	19	19	24+10=34	24+11=35	—	—	—	—
18.5	XIII[1],14	III[1],8	19	19	23+10=33	24+ 9=33	—	—	—	—
19.0	XIII[1],15	III[1],8	19	19	24+10=34	23+10=33	—	—	—	—
19.2	XIII[1],14	III[1],8	19	19	24+10=34	25+10=35	—	—	—	—
19.2	XIII[1],14	III[1],8	19	19	23+10=33	23+10=33	—	—	—	—
20.7	XIII[1],14	III[1],8	19	19	25+10=35	25+10=35	—	—	—	—
20.7	XIII[1],14	III[1],8	19	19	23+10=33	23+10=33	—	—	—	—
21.0	XIII[1],14	III[1],7	19	19	24+10=34	24+10=34	—	—	—	—
22.9	XIII[1],14	III[1],8	19	19	25+10=35	24+10=34	—	—	—	—
[2]23.2	XIII[1],15	III[1],8	19	19	24+10=34	23+10=33	—	—	—	—
[2]24.0	XIII[1],14	III[1],8	19	19	26+11=37	26+11=37	—	—	—	—
[2]24.0	XIII[1],15	III[1],8	19	19	26+10=36	25+10=35	—	—	—	—
[2]24.6	XIII[1],15	III[1],8	19	19	26+10=36	26+10=36	—	—	—	—
[2]27.9	XIII[1],15	III ,8	19	19	26+11=37	27+11=38	—	—	—	—
[3]30.6	XIII[1],14	III ,7	19	19	25+10=35	25+10=35	—	—	—	—
[3]33.1	XIII ,15	III ,8	19	19	28+11=39	27+11=38	—	—	—	—
[3]33.9	XIII ,16	III ,8	19	19	26+12=38	26+11=37	—	—	—	—
[3]35.2	XIII ,15	III ,8	19	19	25+10=35	26+11=37	—	—	—	—
[3]35.8	XIII ,15	III ,8	19	19	25+11=36	25+11=36	—	—	—	—
[3]38.2	XIII ,15	III ,8	19	19	25+11=36	25+11=36	—	—	—	—
[3]39.2	XIII ,15	III ,8	19	19	26+11=37	26+10=36	—	—	—	—
[3]40.0	XIII ,14	III ,8	19	19	27+12=39	26+11=37	—	—	—	—
[3]41.0	XIII ,14	III ,8	19	19	25+10=35	25+10=35	—	—	—	—
[3]43.8	XIII ,15	III ,8	19	19	26+12=38	27+12=39	—	—	—	—
[3]45.3	XIII ,15	III ,8	19	19	26+11=37	26+11=37	—	—	—	—
[3]48.4	XIII ,14	III ,7	19	19	25+10=35	24+11=35	—	—	—	—
[4]52.5	XIII ,14	III ,8	19	19	26+11=37	26+11=37	50	51	54	53
[4]62.5	XIII ,15	III ,8	19	19	27+11=38	28+11=39	48	49	54	57
[4]67.0	XIII ,15	III ,8	19	19	26+11=37	26+11=37	49	46	55	58
[4]76.1	XIII ,14	III ,7	19	19	25+11=36	24+11=35	46	49	49	55
[4]89.4	XIII ,15	III ,8	19	19	26+11=37	26+11=37	51	51	56	56
[4]97.7	XIII ,14	III ,7	19	19	25+11=36	25+10=35	49	51	57	52
[4]100.9	XIII ,15	III ,8	19	19	26+11=37	26+11=37	50	50	53	52
[4]111.6	XIII ,14	III ,8	19	19	24+10=34	24+10=34	49	53	58	55

[1]Posteriormost dorsal or anal spine appears as a soft ray.
[2]Transforming.
[3]Pelagic juvenile.
[4]Benthic juvenile.

mean parietal spine/HL value. This results from many broken parietal spines on pelagic juveniles as indicated in Tables 4, 5.)

The five spines of the posterior preopercular series are present on specimens of both species by ≈11 or 12 mm. The first spine becomes reduced to a small blunt projection by ≈70 mm. The third spine is always longest but decreases in length from 20 to 2 or 3% HL during development. The second, third, and fourth posterior preopercular spines and the anterior edge of the first spine of the anterior preopercular series are weakly serrated on specimens of *S. flavidus* <17 mm and *S. melanops* <16 mm. Serrations persist on the third posterior preopercular spine of both species to ≈32 mm. The second spine of the anterior series is present occasionally (rarely in *S. melanops*) on one side of the head, particularly on specimens <13 mm. The first and third anterior preopercular spines are visible on specimens <27 and 25 mm (*S. flavidus* and *S. melanops*, respectively), become reduced to small bumps, and are no longer visible on specimens >31 and 29 mm.

The inferior opercular spine forms by ≈11 or 12 mm and is sharp tipped by ≈15 or 16 mm. (Two inferior opercular spines were observed on one

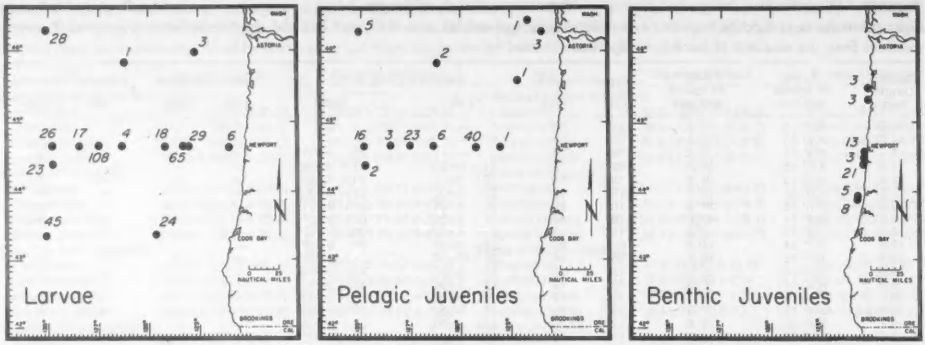

FIGURE 7.—Number of specimens and location of capture of larvae and juveniles of *Sebastes flavidus* off Oregon (1961-78) described in this paper.

side of two specimens of *S. melanops*, 36 and 39 mm long.) The interopercular spine is present on specimens >10 mm and persists as a sharp spine to ≈71 mm on *S. flavidus* and ≈52 mm on *S. melanops*. This spine becomes skin covered and appears as a bump on large specimens.

The ridge anterior to the postocular spine is usually finely serrated on specimens <16 mm in *S. flavidus* and <22 mm in *S. melanops*. Preocular and supraocular spines never develop on either species. The second inferior infraorbital spine is visible as a bump at 10.3 and 11.7 mm on *S. flavidus* and *S. melanops*, respectively, and as a sharp spine by ≈12 mm on both species. A third inferior infraorbital spine appears on both species between 13.5 and 14.5 mm. The second and third inferior spines are reduced to a pair of rounded bony lobes on *S. flavidus* ≈36-67 mm and *S. melanops* 33-50 mm long. *Sebastes flavidus* >67 mm and *S. melanops* >50 mm have a single fleshy lobe which encases the bony lobes. The first superior infraorbital spine is present through the larval periods of both species and becomes reduced and then absent on *S. flavidus* >45 mm and *S. melanops* >38 mm long. The fourth superior infraorbital spine develops by ≈10 mm, is present to ≈45-48 mm, and then is absent in both species. The third superior infraorbital spine appears on *S. flavidus* 15-35 mm and on *S. melanops* 19-33 mm long. A second superior infraorbital spine never develops. The nasal spine appears as a bump between 11 and 12 mm and becomes a sharp spine, between 12 and 13 mm, which persists on all larger specimens of both species.

The tympanic spine never becomes well developed, appearing as a small bump on ≈24-63 mm *S. flavidus* and 30 to ≈40 mm *S. melanops* and as a small spine on larger specimens. The pterotic spine is present on all larvae <24 mm; is usually a bump on specimens 24-41 mm; and is absent on larger specimens. The inferior posttemporal spine is reduced to a bump and then absent on *S. flavidus* >67 mm and *S. melanops* >45 mm. The supracleithral spine and superior posttemporal spine first appear at ≈11 or 12 and ≈19 or 20 mm, respectively, and persist in benthic juveniles. These spines are scale covered on benthic juvenile *S. melanops* >67 mm. The cleithral spine usually appears as a bump at ≈24 mm in *S. flavidus* and at ≈30 mm in *S. melanops*. Specimens >33 mm have a sharp spine which is scale covered in larger juvenile and adult *S. flavidus* and *S. melanops* >67 mm long.

Scale Formation.—Lateral line organs are visible on transforming specimens >14.8 mm in *S. flavidus* and >17.2 mm in *S. melanops*, indicated by a row of light colored spots on the flesh. Developing scales are first visible on unstained specimens ≈23 or 24 mm long in the region above the pectoral fin, near the posttemporal and supracleithral spines, and over the upper two-thirds of the body in the postanal region. The body is scale covered by ≈28 mm.

Pigmentation.—The smallest larvae (10.1 and 10.6 mm) of both *S. flavidus* and *S. melanops* have melanistic pigment on the head over the brain. Melanophores are usually present on the

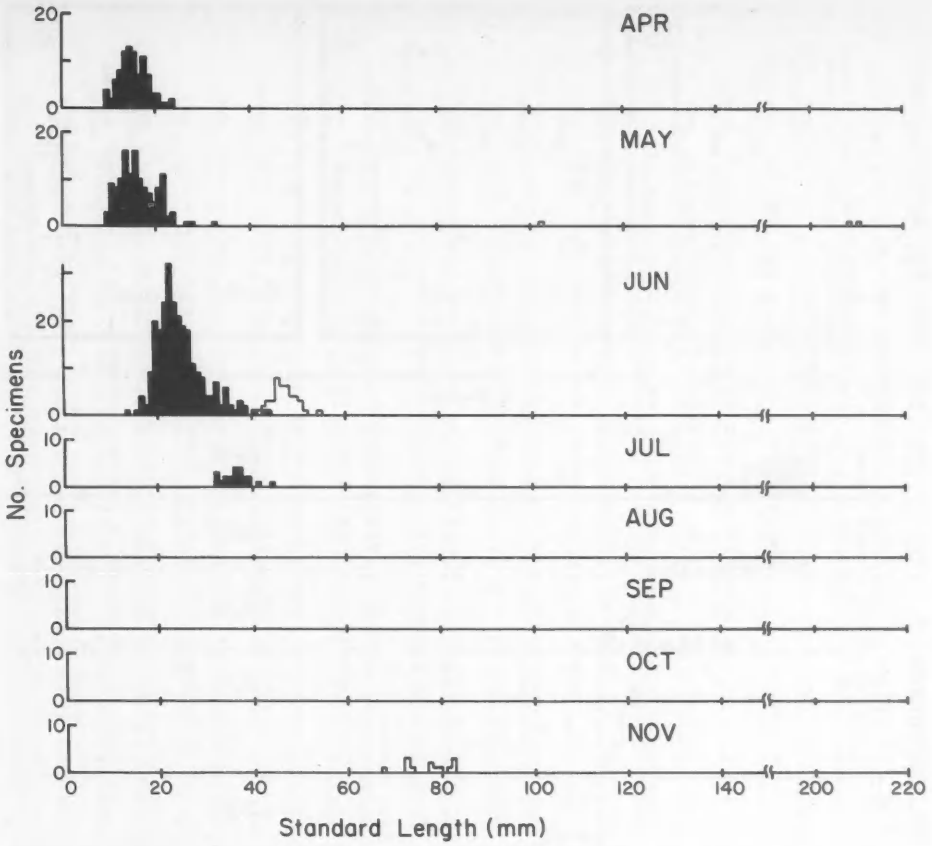

FIGURE 8.—Seasonal occurrence of larvae and juveniles of *Sebastes flavidus* off Oregon. Data from 1961 to 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

inside tip of the lower jaw, along the anterior margin of the maxillary, around the pterotic spines, and on the operculum. The 10.6 mm larva of *S. melanops* also has pigment on the snout, along the posteroventral margin of the orbit, on the cheek, and around the posttemporal spine. An internal melanistic shield covers the gut in both species appearing darkest on the dorsal surface. In *S. flavidus* melanophores are present dorsally on the nape, beneath the second dorsal fin, and on the caudal peduncle. In addition to these, *S. melanops* has melanophores beneath the first dorsal fin, possibly due to a more advanced state of development for this specimen. Several melanophores also occur along the posterior portion of the anal fin base and the ventral margin of the caudal peduncle in both species. Internal and external melanophores are present near the midline of the caudal peduncle and several melanophores are at the margin of the hypural elements. The pectoral and pelvic fin blades are moderately pigmented with expanded, elongated melanophores. The inner side of the pectoral base is also pigmented. A discrete melanophore is pres-

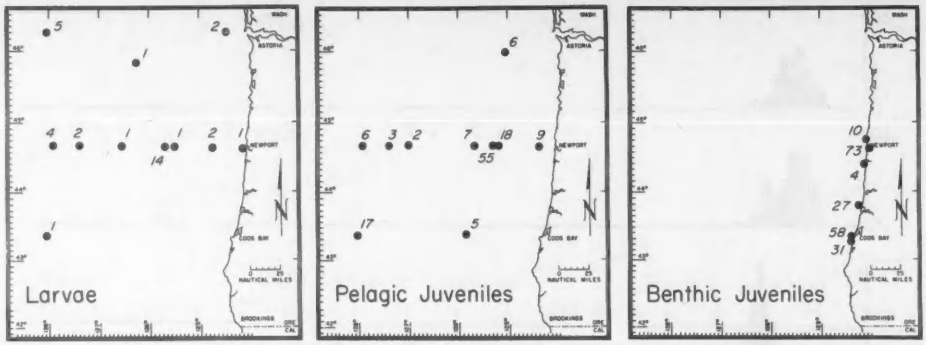

FIGURE 9.—Number of specimens and location of capture of larvae and juveniles of *Sebastes melanops* off Oregon (1961-78) described in this paper.

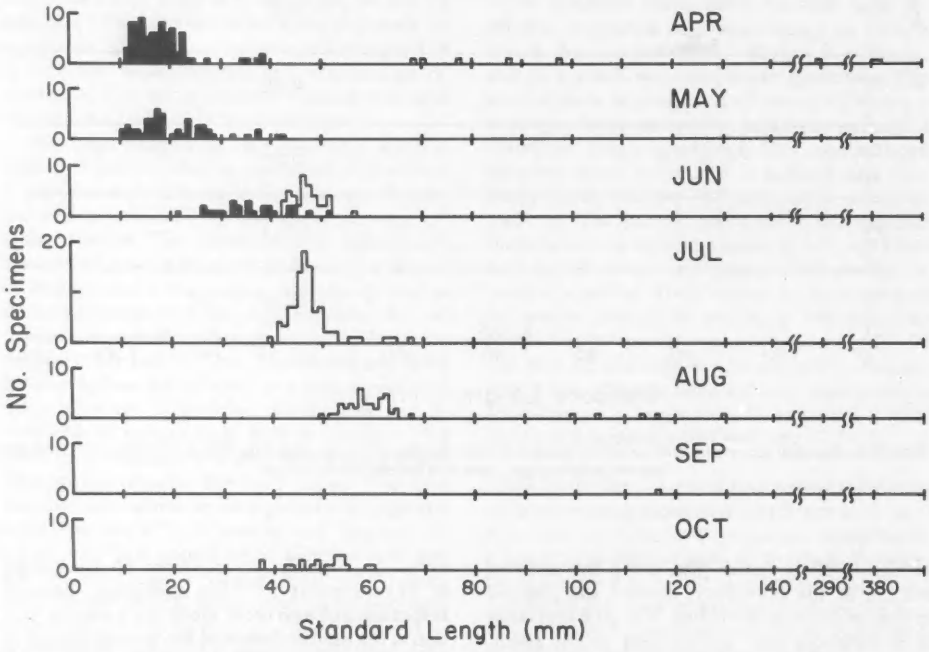

FIGURE 10.—Seasonal occurrence of larvae and juveniles of *Sebastes melanops* off Oregon. Data from 1961 to 1978 combined. Solid bars indicate pelagic stages, open bars indicate benthic stages.

ent at the articulation of each of several dorsal and anal fin rays (more in the 10.6 mm *S. melanops* than in the 10.1 mm *S. flavidus*).

As larvae develop, pigment increases over the brain. Melanophores are added on the snout, interorbital region, tips of the upper and lower lips,

TABLE 4.—Measurements (millimeters) of larvae and juveniles of *Sebastes flavidus* from waters off Oregon.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal to hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
10.1	12.5	5.5	4.0	1.2	1.7	—	1.1	3.0	2.2	1.1	1.7	1.6	1.1	0.64	0.90	3.9	0.44	—	1.08	—	0.20	0.76	([4])
10.3	13.3	6.3	4.4	1.3	1.9	1.5	1.3	3.1	2.3	1.3	1.6	2.1	1.0	0.83	1.2	4.4	0.50	0.02	—	—	0.57	1.2	0.52
10.7	13.7	5.9	4.3	1.2	1.9	1.4	1.3	3.2	2.4	1.2	1.8	2.0	1.0	0.78	1.1	4.2	0.34	0.04	0.96	—	0.56	1.3	0.48
11.4	14.6	6.6	4.6	1.2	2.0	1.6	1.4	3.4	2.7	1.4	1.8	2.4	1.1	1.1	1.4	4.6	0.44	0.04	0.96	—	0.68	1.2	0.64
11.8	15.0	6.8	4.7	1.2	2.0	1.6	1.4	3.5	2.6	1.4	1.7	1.9	1.1	1.1	1.5	4.7	0.49	—	1.00	—	0.70	1.2	1.00
11.8	15.2	7.1	4.8	1.4	2.1	1.7	1.4	3.5	2.8	1.4	1.7	2.3	1.1	1.3	1.8	4.8	0.53	0.06	—	—	—	—	—
11.9	15.1	6.6	4.7	1.3	1.9	1.5	1.5	3.5	2.5	1.4	1.8	2.2	1.1	0.98	1.4	4.3	0.54	0.04	—	—	0.64	1.3	0.52
12.0	15.0	6.7	4.9	1.3	2.0	1.5	1.5	3.7	2.9	1.5	2.0	2.4	1.0	1.2	1.6	4.6	0.43	0.14	0.98	—	0.76	1.4	0.66
12.2	15.8	6.9	4.8	1.3	2.0	1.7	1.5	3.6	2.8	1.5	1.8	2.4	1.1	1.2	1.6	4.6	0.49	0.05	0.92	—	0.90	1.4	0.92
12.7	—	6.8	5.1	1.4	—	1.7	1.5	3.4	2.8	1.4	1.7	2.4	1.1	1.3	1.6	5.1	0.43	0.07	—	0.54	0.86	1.4	—
12.8	16.3	7.2	5.0	1.3	2.1	1.7	1.5	3.7	2.8	1.5	1.9	2.4	1.1	1.2	1.6	4.8	0.43	0.06	1.04	0.64	0.84	1.3	1.04
12.9	16.6	7.3	4.9	1.5	2.2	1.6	1.5	3.8	3.0	1.5	2.1	2.7	1.1	1.2	1.7	4.9	0.58	0.06	1.17	0.53	0.88	1.5	1.17
13.1	16.7	7.6	4.9	1.4	2.1	1.6	1.5	3.8	3.0	1.5	2.0	2.5	1.1	1.3	1.7	5.0	—	([5])	1.00	0.44	0.83	1.5	1.00
13.7	17.5	7.8	5.3	1.6	2.1	1.6	1.6	4.0	3.2	1.6	2.1	2.8	1.2	1.4	1.9	5.0	0.46	0.17	1.10	0.68	0.96	1.6	1.10
14.4	18.1	8.4	5.3	1.5	—	1.7	1.5	4.0	3.2	1.5	2.0	2.6	1.2	1.4	1.6	5.6	0.53	0.16	1.15	0.58	0.96	1.6	1.15
14.8	—	8.8	5.9	1.5	2.3	1.8	1.7	4.0	3.2	1.6	2.3	3.2	1.2	—	2.1	5.6	—	0.18	—	0.68	1.2	1.8	—
15.8	20.0	8.8	5.9	1.7	2.4	1.6	1.6	4.0	3.3	1.7	2.6	3.0	1.2	1.2	1.9	5.8	—	—	—	0.70	0.96	1.8	0.64
15.9	20.0	9.2	6.1	1.7	2.6	1.8	1.7	4.6	3.8	1.9	2.6	3.4	1.3	1.9	2.5	6.0	0.60	0.20	1.22	0.66	1.4	2.0	1.2
16.4	20.7	9.6	6.1	1.7	2.8	2.0	1.7	4.2	3.6	1.8	2.7	3.4	1.3	2.2	2.4	5.9	0.50	0.18	—	0.78	1.6	1.8	1.3
16.8	21.7	9.8	6.3	1.7	2.7	2.0	1.7	4.8	3.9	1.9	2.6	3.8	1.4	—	2.5	6.3	0.54	—	—	0.80	1.8	2.4	—
18.9	24.0	10.7	6.7	1.8	2.8	2.0	1.9	4.8	3.9	2.1	2.9	3.7	1.4	—	2.6	6.5	0.49	0.18	—	0.80	—	2.2	—
19.5	25.1	11.5	7.2	1.8	3.1	2.3	2.0	5.1	4.2	2.0	3.0	4.4	1.4	2.8	3.1	7.3	0.38	—	1.16	1.00	2.1	2.7	1.6
19.8	25.6	11.5	7.1	1.7	3.2	2.3	1.9	5.4	4.2	2.1	3.2	4.5	1.6	3.1	3.3	7.6	0.40	0.28	1.26	1.00	2.3	2.6	1.8
20.5	26.1	11.5	7.6	1.9	3.4	2.3	2.0	5.4	4.4	2.2	3.2	4.6	1.5	3.0	3.2	7.3	0.32	0.22	1.23	0.90	2.3	2.7	2.0
21.3	26.3	12.5	8.0	2.1	3.2	2.4	2.0	5.6	4.5	2.2	3.3	4.8	1.6	2.7	3.1	7.8	—	0.16	—	1.16	—	2.7	—
22.3	28.3	12.9	8.1	2.2	3.6	2.4	2.1	5.8	4.9	2.3	3.4	5.0	1.6	—	3.1	7.9	0.44	0.26	1.04	1.10	2.3	3.0	2.0
[6]23.6	—	14.1	8.4	2.2	3.5	2.5	2.2	5.7	4.8	2.4	3.7	5.4	1.6	3.4	3.8	8.5	—	0.22	1.34	1.17	2.7	3.3	2.3
[6]23.7	—	13.7	8.4	2.2	3.7	2.5	2.1	5.6	4.9	2.3	3.6	5.1	1.7	3.2	3.7	8.5	—	—	1.18	1.18	2.6	3.0	2.2
[6]24.2	30.7	14.0	8.7	2.3	3.5	2.5	2.1	6.2	4.9	2.4	3.7	5.6	1.7	3.7	3.8	8.6	0.30	0.16	1.20	1.24	3.0	3.3	2.5
[6]24.8	31.4	15.0	8.8	2.3	3.3	2.5	2.2	6.1	5.0	2.5	3.6	5.5	1.8	3.4	4.0	9.0	—	0.20	1.02	1.42	3.0	3.1	2.4
[6]25.6	31.5	15.4	9.0	2.3	3.6	2.6	2.2	6.3	5.1	2.4	4.0	5.7	1.8	3.4	3.8	9.4	0.42	—	1.04	1.3	3.1	—	2.3
[6]26.6	31.7	15.3	9.0	2.4	3.8	2.5	2.2	6.4	5.1	2.4	3.8	5.7	1.8	3.4	4.1	9.4	0.34	0.18	0.90	1.4	2.8	3.3	2.0
[6]26.7	32.9	15.8	9.0	2.4	3.4	2.6	2.2	6.6	5.2	2.5	4.1	6.5	1.8	3.4	3.9	9.5	—	0.18	—	1.3	2.9	3.2	—
[7]28.5	36.2	17.4	10.3	3.0	4.3	2.9	2.6	6.9	6.0	2.8	4.2	—	2.0	4.4	4.9	10.6	0.18	—	1.34	1.2	3.5	4.0	2.7
[7]29.2	36.0	17.4	10.2	2.8	4.0	2.7	2.6	7.1	5.9	2.8	4.2	—	1.9	3.8	—	10.4	—	0.24	—	1.4	—	—	2.8
[7]29.6	37.0	17.5	9.8	2.6	4.2	2.8	2.5	6.9	5.9	2.9	4.4	—	1.8	—	4.8	10.5	—	—	—	1.4	3.3	3.9	3.1
[7]30.4	—	18.4	10.5	2.6	4.4	2.7	2.6	7.6	6.5	3.0	5.4	7.6	2.3	—	5.4	11.0	—	0.24	—	1.7	3.8	—	3.2
[7]33.0	41.3	19.8	10.6	2.7	4.4	2.9	2.8	7.8	6.6	3.1	5.0	8.1	2.3	4.7	5.1	12.1	—	0.12	1.24	1.6	3.8	4.7	3.3
[7]33.1	—	19.7	10.7	2.6	4.5	3.1	3.0	7.9	7.3	3.2	5.0	—	2.3	4.6	5.5	12.0	—	—	1.18	1.6	4.2	—	3.6
[7]35.2	44.3	21.4	11.7	2.7	5.1	3.4	3.0	9.0	7.5	3.3	5.2	8.6	2.6	4.9	5.3	12.5	—	—	1.24	1.6	4.2	4.7	—
[7]36.4	45.5	21.4	12.4	3.0	5.1	3.2	2.9	9.1	7.6	3.5	6.0	8.9	2.5	4.9	6.2	13.2	0.10	([8])	1.08	1.8	4.3	4.6	3.9
[7]37.6	45.9	22.4	12.0	3.1	5.1	3.2	2.8	10.1	8.8	3.9	5.3	9.3	2.8	—	6.1	13.4	([8])	—	1.16	1.7	4.2	4.6	—
[7]41.9	51.8	26.1	14.4	3.9	6.0	3.7	3.4	10.9	8.9	3.9	6.0	10.5	2.7	5.7	6.2	15.8	0.10	—	1.12	2.2	4.9	5.7	4.6
[7]43.6	—	26.6	14.2	3.7	6.3	3.7	3.5	11.2	9.5	4.2	6.3	10.5	3.2	5.5	7.1	15.4	0.10	—	1.30	2.0	—	—	4.7
[7]45.2	55.6	27.7	14.4	3.4	6.2	3.9	3.5	11.0	9.9	4.4	6.7	11.0	3.2	5.7	7.6	16.4	([8])	—	1.40	2.2	4.9	6.6	4.1
[8]67.6	79.3	42.4	22.7	7.2	9.7	6.7	5.0	19.2	15.9	6.9	9.8	16.0	5.9	—	13.4	27.8	0.14	—	1.08	3.5	8.2	9.3	7.9
[8]71.5	85.7	44.5	24.9	5.7	10.2	6.5	5.4	22.1	18.5	7.5	9.0	18.4	6.0	8.4	13.7	26.9	([8])	—	0.72	4.0	8.8	10.8	8.5
[8]72.5	88.9	45.4	25.4	8.3	11.5	6.7	5.5	22.0	18.2	8.0	9.5	17.5	6.3	8.2	14.0	27.0	([8])	—	0.60	3.7	8.7	11.7	9.1
[8]77.5	94.5	48.8	25.9	7.0	10.4	7.0	5.8	22.7	20.4	8.1	10.7	18.2	6.4	9.5	15.0	29.5	([8])	—	0.96	3.9	9.5	11.5	8.4
[8]81.0	98.9	53.1	29.0	8.7	11.4	7.0	6.2	25.1	21.4	8.7	9.7	19.9	6.3	10.7	16.5	33.3	([8])	—	1.00	4.2	9.2	11.7	9.9
[8]105.0	125.8	66.1	35.3	10.0	16.4	9.7	8.5	31.8	27.4	10.4	13.7	22.9	9.0	12.7	20.0	45.1	—	—	0.92	5.1	11.9	16.0	12.5

[1]Usually fourth or fifth in larvae, fifth or sixth in juveniles.
[2]Usually in anterior one-fourth of fin.
[3]The second spine in larvae, the third spine in juveniles.
[4]Forming.
[5]Bump.
[6]Transforming.
[7]Pelagic juvenile.
[8]Benthic juvenile.

along the maxillary, and on the cheek and operculum. Pigment increases around the orbit (eventually lining it), and around the posttemporal spine, extending anteriorly over the head. Melanophores line the anterior margin of the cleithrum beneath the operculum.

Pigment on the gut becomes less intense as body musculature increases. The dorsal body surface is pigmented from nape to caudal peduncle in both species by 11 mm. Large stellate melanophores beneath the soft dorsal fin increase in number and are aligned along the muscles surrounding the dorsal pterygiophores, sometimes appearing as lines of pigment. This is the densest pigmentation on larvae. Internal and external melanophores are added along the body midline anteriorly from the caudal peduncle forming a line along the notochord which extends to the head by ≈14 or 15 mm. Melanophores extend ventrolaterally from the nape to the lateral midline by ≈14-16 mm and are added posteriorly along the dorsolateral body surface with development. Initially these melanophores appear along the myosepta, but this pattern becomes obscured as

TABLE 5.—Measurements (millimeters) of larvae and juveniles of *Sebastes melanops* from waters off Oregon.

Standard length	Total length	Snout to anus length	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth at pectoral fin base	Body depth at anus	Caudal peduncle depth	Dorsal to hypural distance	Pectoral fin length	Pectoral fin base depth	Pelvic spine length	Pelvic fin length	Snout to pelvic fin origin	Parietal spine length	Nuchal spine length	Preopercular spine length	Angle gill raker length	Longest dorsal spine length[1]	Longest dorsal ray length[2]	Longest anal spine length[3]
10.6	13.7	6.1	4.4	1.2	1.9	1.5	1.2	3.2	2.5	1.4	1.7	2.0	1.0	1.0	1.5	4.2	0.50	[4]	—	—	0.69	1.10	0.58
11.7	15.0	6.8	4.8	1.2	—	1.5	1.4	3.6	3.0	1.6	1.9	2.3	1.1	1.2	1.5	4.7	0.50	[4]	1.02	0.35	0.74	1.34	0.70
11.9	15.4	7.4	5.1	1.3	2.1	1.6	1.5	3.8	3.1	1.7	1.8	2.4	1.2	1.3	1.6	4.9	—	[4]	—	0.48	0.86	1.28	0.64
11.9	15.2	6.9	4.6	1.3	2.1	1.5	1.4	3.7	2.9	1.6	1.8	2.2	1.2	1.1	1.5	4.7	0.44	[4]	—	0.42	0.70	1.30	0.52
12.4	16.4	7.3	4.9	1.3	2.1	1.5	1.6	4.0	3.2	1.7	1.9	2.8	1.2	1.5	1.8	4.6	—	0.04	—	0.48	0.96	1.56	0.78
12.8	16.9	7.7	5.2	1.3	2.3	1.7	1.5	4.0	3.3	1.8	1.7	2.9	1.2	1.5	1.9	4.9	0.58	0.04	1.40	0.50	1.20	1.68	0.90
12.8	16.7	7.6	5.1	1.4	2.1	1.6	1.5	4.2	3.3	1.8	1.8	2.7	1.2	1.4	1.9	4.9	0.46	0.03	1.20	0.46	0.94	1.60	0.84
12.8	16.8	7.6	5.1	1.6	2.2	1.6	1.6	4.1	3.2	1.8	1.8	2.8	1.2	1.4	1.8	4.9	0.52	0.04	1.24	0.49	0.90	1.80	0.78
13.5	—	7.8	5.4	1.4	2.4	1.6	1.7	4.4	3.5	1.9	1.9	2.9	1.3	1.5	2.1	4.9	0.40	0.04	1.14	0.56	—	1.40	0.98
13.6	17.4	8.4	5.4	1.4	2.3	1.7	1.7	4.2	3.4	1.8	2.2	3.0	1.3	1.8	2.3	4.9	—	0.02	1.26	0.58	1.22	1.60	1.00
13.9	17.7	8.2	5.6	1.7	2.4	1.8	1.7	4.2	3.5	1.8	2.1	2.8	1.2	1.7	2.0	5.3	0.54	0.06	1.30	0.58	1.08	1.66	0.84
14.0	18.6	8.4	5.6	1.7	2.5	1.8	1.7	4.3	3.6	2.0	2.1	3.1	1.3	1.8	2.1	6.0	0.52	0.06	1.24	0.57	1.24	2.02	1.00
14.9	19.9	8.8	6.1	1.7	2.6	1.8	1.8	4.5	3.8	1.8	2.2	3.1	1.4	2.0	2.4	5.9	0.52	0.08	1.36	0.70	1.46	2.10	1.06
15.4	19.5	9.5	6.0	1.7	2.5	1.8	1.7	4.6	3.7	2.0	2.2	3.0	1.4	1.9	2.4	6.3	0.44	0.08	1.20	0.68	1.24	2.16	1.08
15.4	—	9.2	6.0	1.7	2.4	1.8	1.7	4.6	3.6	2.0	2.4	3.3	1.4	2.0	2.3	6.3	0.34	0.10	1.18	0.67	—	1.92	—
15.7	20.6	9.4	5.8	1.7	2.5	1.9	1.8	4.5	3.7	1.9	2.3	3.3	1.3	2.0	2.4	6.1	—	[4]	1.20	0.56	1.14	1.80	1.12
15.9	20.5	9.6	6.0	1.7	2.4	1.8	1.9	4.7	3.8	2.0	2.2	3.4	1.4	—	2.4	6.4	—	[4]	1.16	0.64	1.52	—	—
16.4	21.1	9.5	6.5	1.7	2.7	2.0	1.7	4.6	3.8	2.0	2.3	—	1.4	2.3	2.6	6.1	0.48	0.20	1.03	0.78	1.76	—	1.28
16.5	21.6	9.2	6.0	1.7	2.9	2.0	1.8	4.9	4.2	2.1	2.5	3.6	1.4	2.3	2.5	6.1	0.38	0.08	1.34	0.74	1.70	2.30	1.48
17.2	22.1	9.6	6.6	1.9	2.7	2.0	1.8	4.9	4.0	2.2	2.5	3.7	1.4	2.3	2.5	6.9	0.46	[4]	1.17	0.76	1.68	2.20	1.38
17.4	22.4	9.4	6.3	1.7	2.4	2.0	1.9	5.2	4.3	2.2	2.5	4.0	1.6	2.6	2.8	7.0	—	[4]	1.20	0.80	1.86	2.20	1.46
17.4	22.0	10.0	6.6	1.8	2.8	1.9	2.0	4.9	4.1	2.1	2.6	4.1	1.5	2.5	2.8	6.5	—	0.08	1.20	0.89	—	2.32	1.40
17.7	23.1	9.9	6.3	1.7	2.5	2.1	2.0	5.2	4.6	2.3	2.6	4.2	1.6	2.1	2.8	6.6	0.46	0.10	—	0.78	1.60	2.30	1.30
17.7	22.0	10.2	6.5	1.9	2.8	2.1	1.9	5.1	4.0	2.1	2.4	3.9	1.5	2.5	2.8	6.6	0.56	[4]	1.10	0.70	1.76	2.16	1.46
18.5	23.4	10.6	7.0	1.9	3.0	2.1	2.0	5.1	4.2	2.3	2.4	4.2	1.6	2.4	3.0	7.0	—	—	1.30	0.94	1.98	2.50	1.64
19.0	—	10.6	6.9	2.0	2.8	2.1	2.0	5.5	4.5	2.2	2.7	4.5	1.5	2.5	3.2	6.8	—	0.22	1.12	0.72	1.90	—	1.56
19.2	24.7	10.9	7.2	1.9	3.0	2.2	2.0	5.2	4.5	2.3	2.7	4.7	1.6	2.8	3.3	7.6	0.53	0.20	1.27	0.86	2.10	2.40	—
19.2	24.4	10.8	7.5	1.9	3.0	2.2	1.8	5.1	4.5	2.2	2.4	4.3	1.5	2.6	3.0	7.0	0.44	0.22	1.10	0.76	1.84	2.38	1.66
20.7	25.8	11.4	7.6	2.1	3.2	2.2	2.0	5.8	5.0	2.5	3.0	4.7	1.6	3.0	3.4	8.4	0.32	0.16	1.10	0.90	2.26	2.68	—
20.7	25.9	12.0	7.2	2.1	3.1	2.2	2.0	5.8	4.7	2.5	2.8	4.7	1.7	2.8	3.6	8.3	0.36	0.18	1.26	0.80	2.30	—	—
21.0	25.9	12.3	7.8	2.3	3.1	2.1	2.0	6.1	4.9	2.5	2.9	4.4	1.7	3.1	3.4	8.8	—	—	1.22	0.90	2.40	—	2.0
22.9	27.8	12.3	8.3	2.3	3.1	2.3	2.1	6.1	5.0	2.6	3.5	4.8	1.8	2.9	3.8	8.9	—	—	1.21	1.02	2.60	3.00	2.1
[5]23.2	—	12.9	8.3	2.1	3.4	2.5	2.2	6.1	5.2	2.7	3.2	5.2	1.8	2.4	3.8	8.3	0.50	0.17	—	0.90	2.28	3.10	2.0
[5]24.0	—	13.4	8.6	2.4	3.6	2.4	2.3	6.1	5.2	2.8	3.4	5.9	1.8	2.9	4.0	8.6	0.46	—	1.24	0.96	—	3.00	—
[5]24.0	30.6	13.4	8.5	2.2	3.6	2.6	2.2	6.6	5.6	2.8	3.5	5.6	1.9	2.6	4.0	9.0	—	0.20	1.06	0.90	—	3.00	2.3
[5]24.6	—	15.4	9.3	2.6	3.5	2.6	2.3	6.6	5.4	2.7	3.5	5.6	1.9	—	—	10.2	—	[4]	1.10	1.01	—	—	—
[5]27.9	—	16.7	8.9	2.3	3.7	2.7	2.4	7.2	6.0	3.0	4.0	6.6	2.1	—	4.5	9.7	0.52	—	1.26	1.20	—	—	2.8
[5]30.6	39.4	18.5	10.4	2.7	4.4	2.7	2.6	7.7	6.4	3.2	4.4	7.8	2.4	—	5.0	11.9	—	0.30	1.40	1.56	—	4.2	3.4
[5]33.1	—	20.2	11.7	3.1	4.6	2.9	2.7	8.6	7.3	3.4	4.8	8.3	2.6	4.8	5.6	12.1	—	—	1.28	1.64	4.1	4.5	3.5
[5]33.9	42.1	21.0	11.9	3.5	4.9	3.1	2.8	9.0	7.5	3.5	4.8	8.3	2.6	5.0	5.8	13.4	[4]	—	—	1.56	4.2	—	3.8
[5]35.2	43.8	20.9	11.7	2.8	4.9	3.2	2.9	8.7	7.5	3.6	4.8	8.4	2.7	4.9	5.9	12.4	[4]	—	—	1.64	4.6	4.6	4.0
[5]35.8	44.3	21.7	11.4	2.8	5.0	3.3	2.9	9.3	7.9	3.6	4.7	8.9	2.8	5.1	6.3	12.6	0.08	—	1.24	1.68	4.5	4.9	3.7
[5]38.2	48.2	23.4	12.8	3.2	5.1	3.2	3.1	10.1	8.4	4.0	5.2	9.4	2.9	5.3	6.6	14.0	0.20	—	1.24	1.72	4.6	4.9	4.2
[5]39.2	49.0	23.3	12.2	3.2	4.9	3.3	3.2	9.8	8.2	3.8	5.3	9.3	3.0	5.6	7.1	14.0	[4]	—	—	1.96	4.8	5.0	4.1
[5]40.0	—	24.0	12.9	3.5	5.7	3.4	3.2	10.3	9.0	4.2	5.8	9.5	3.2	5.8	7.3	14.3	0.16	—	1.30	1.76	—	—	3.9
[5]41.0	—	25.4	13.0	3.4	5.3	3.6	3.3	10.9	9.2	4.3	6.1	9.2	3.2	5.7	7.3	14.9	[4]	—	—	2.06	—	—	4.9
[5]43.8	53.9	27.2	15.0	4.5	6.3	3.6	3.4	11.7	10.0	4.6	6.3	10.1	3.4	5.6	7.4	16.0	0.20	—	1.26	2.00	5.0	—	4.3
[5]45.3	55.7	27.9	15.4	4.3	6.6	4.2	3.7	11.9	10.7	4.7	5.8	11.4	3.6	6.1	8.4	17.0	0.18	—	1.48	2.12	5.5	6.2	4.8
[5]48.4	59.6	31.6	16.7	5.0	6.6	4.2	3.7	12.2	10.9	4.8	6.9	12.1	3.8	6.5	8.5	19.4	0.28	—	1.48	2.18	—	6.7	5.5
[6]52.5	64.1	37.1	17.2	4.2	7.3	4.6	4.5	15.4	13.3	6.1	7.0	13.2	4.9	6.5	10.5	20.0	—	—	0.78	2.72	6.5	8.3	6.1
[6]62.5	75.6	37.5	20.2	4.8	8.9	5.0	5.3	16.9	16.0	7.0	8.4	14.5	5.9	6.7	12.0	23.0	—	—	0.32	3.20	7.4	8.3	6.5
[6]67.0	80.8	41.6	22.4	5.2	10.4	5.4	5.4	21.2	18.2	7.8	8.9	15.7	6.5	7.8	12.5	23.7	—	—	0.10	3.28	7.6	10.3	7.0
[6]76.1	93.3	48.0	27.9	6.3	13.4	7.3	5.9	23.7	20.0	8.4	9.5	20.7	7.2	9.5	15.9	31.8	—	—	0.52	3.92	9.8	12.9	9.9
[6]89.4	110.3	56.5	31.0	8.2	15.0	8.9	7.5	28.1	24.0	9.9	10.4	22.9	8.4	12.0	19.7	37.1	—	—	0.83	4.81	11.0	14.0	11.0
[7]97.7	118.5	58.0	36.4	8.5	15.9	9.0	7.7	30.4	25.5	10.9	12.4	22.4	8.3	12.5	19.9	37.2	—	—	0.88	5.15	12.4	16.7	12.9
[7]100.9	123.0	63.0	36.1	7.2	16.4	9.5	8.4	33.3	27.6	11.4	12.5	26.4	9.5	14.0	23.2	38.0	—	—	0.80	5.31	13.0	17.5	13.4
[7]111.6	135.5	70.0	39.4	8.4	17.0	9.2	8.9	36.5	30.0	12.4	13.2	26.7	10.9	15.5	24.0	39.9	—	—	1.00	5.73	13.5	18.7	14.0

[1]Usually fourth or fifth in larvae, fifth or sixth in juveniles.
[2]Usually in anterior one-fourth of fin.
[3]The second spine in larvae, the third spine in juveniles.
[4]Bump.
[5]Transforming.
[6]Pelagic juvenile.
[7]Benthic juvenile.

melanophores are added between myosepta, particularly along the dorsal one-fourth of the body. Some melanophores remain visible along the ventral margin of the caudal peduncle although they eventually become internal and obscured by tissues. Melanophores are added along the base of the anal fin. Discrete melanophores are added at the articulation of dorsal and anal fin rays and

spines until most of them have a melanophore. Melanophores are added along the caudal fin base, often appearing as a line, and onto the fin membrane. Pigment decreases on the pectoral and pelvic fins and is usually absent on larvae by ≈16-20 mm.

During the transformation period, ≈23-27 mm in *S. flavidus* and ≈23-31 mm in *S. melanops*, pigment gradually increases over the head and body. Melanophores are added on the lips, lower jaw, snout, and dorsolateral areas of the head. Pigment becomes continuous around the orbit. Melanophores are added ventrolaterally beneath the midline band and increase along the ventral body surface above the anal fin.

Pelagic juveniles, ≈28-56 mm in *S. flavidus* and ≈33-52 mm in *S. melanops*, undergo a general increase in pigment with development. The upper head, snout, lips, lower jaw, maxillary, cheek, and gular region become increasingly pigmented with small melanophores. Opercular pigmentation appears less distinct due to scale covering at ≈33 mm. On the side of the body, melanophores are added ventrolaterally until all but the ventral one-eighth is pigmented. Small melanophores increase in number along the ventral surface of the caudal peduncle. Melanophores are added anteriorly and proximally on the first dorsal fin and are eventually scattered over it. A dark blotch develops in the posterior portion of the spinous dorsal fin by ≈35 mm and persists on all larger pelagic juveniles. Melanophores are added to the proximal half of the soft dorsal fin. A few scattered melanophores are added to the pectoral fin and proximal half of the caudal fin. Pigment distinctly lines the caudal fin base.

Benthic juveniles, >60 mm, have essentially the same melanistic pigment pattern as the largest pelagic juveniles. Pigmentation at the anterior tips of the lips and along the ventral edge of the maxillary intensifies and a dark bar extends from the posteroventral margin of the eye across the cheek. In *S. melanops* a second dark bar forms dorsal to the first and extends from the eye across the opercle becoming distinct by 76 mm. Melanophores appear on patches of scales covering the dorsal half of the body in both species. These patches overlie the pigment described for pelagic juveniles creating darker patches with lighter areas interspersed where pigmentless scales overlie pigmented areas. The dorsal half of the body has a mottled appearance as a result of this. Melanophores first appear on the pectoral fin base of *S. flavidus* in a patch which extends onto the fin membrane and on the underside of the fin base. Later, additional small melanophores lightly cover the pectoral, anal, and caudal fins while only a few small melanophores appear on the pelvic fin. Benthic juvenile *S. melanops* have melanophores covering all fins, however, the distal margins of those in smaller specimens are usually pigmentless. Although already covered by melanophores, the pectoral fin in small benthic (<63 mm) *S. melanops* has a patch of large melanophores which spread over the dorsal half of the pectoral ray bases and adjacent fin base in the same area which first appears pigmented on the pectoral fin of *S. flavidus*. The spinous dorsal fin, anterior to the black blotch, appears mottled in *S. melanops*. On the soft dorsal fin a more lightly pigmented bar runs through the proximal third of the fin. This bar becomes faint or indistinguishable on specimens >67 mm long. Previously described pelagic juvenile body pigment along the anal fin base, at the articulation of the anal fin rays, and on the caudal peduncle becomes completely obscured by scales and tissues on both species, and small melanophores on the scales are alone visible. In general benthic juvenile *S. flavidus* are more lightly pigmented than *S. melanops* taken over similar substrate, however, the pigment patterns are very similar.

Color of Fresh Specimens.—Yellow chromatophores are visible interspersed with melanophores over all body surfaces on pelagic and benthic juveniles of both *S. flavidus* and *S. melanops*. In *S. melanops* they are not numerous enough to give the fish a distinctly yellow cast. The concentration of yellow chromatophores is generally greatest in the areas where melanistic pigment is densest, e.g., the base of the caudal fin, the pigment bar radiating from the posteroventral margin of the eye, darker areas on fins. Yellow pigment is not concentrated around the dorsal fin black blotch. Juveniles generally appear darkly mottled with faintly yellow fins, yellowish areas on the head and body, and cream colored ventrally. However, considerable variation in the intensity of the melanistic pigment of benthic juveniles may occur seemingly dependent upon bottom substrate. When melanistic pigment is less intense, yellow pigment is more outstanding. The yellow tail,

TABLE 6.—Development of spines in the head region of *Sebastes flavidus* larvae and juveniles. + denotes spine present and − denotes spine absent.

Standard length (mm)	Parietal	Nuchal	Preopercular (anterior series)			Preopercular (posterior series)					Opercular		Interopercular	Subopercular	Preocular	Supraocular	Postocular
			1st	2d	3d	1st	2d	3d	4th	5th	Superior	Inferior					
10.1	+	+	+	−	+	+	+	+	+	−	+	−	(1)	−	−	−	+
10.3	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
10.7	+	+	+	+	+	+	+	+	+	−	+	−	+	−	−	−	+
11.4	+	+	+	+	+	+	+	+	+	(1)	+	−	+	−	−	−	+
11.8	+	−	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
11.8	+	+	+	−	+	+	+	+	+	(1)	+	−	+	−	−	−	+
11.9	+	+	+	+	+	+	+	+	+	+	+	(1)	+	−	−	−	+
12.0	+	+	+	+	+	+	+	+	+	+	+	(1)	+	−	−	−	+
12.2	+	+	+	−	+	+	+	+	+	+	+	(1)	+	−	−	−	+
12.7	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
12.8	+	+	+	+	+	+	+	+	+	+	+	(1)	+	−	−	−	+
12.9	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
13.1	+	(1)	+	−	+	+	+	+	+	+	+	(1)	+	−	−	−	+
13.7	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
14.4	+	+	+	−	+	+	+	+	+	+	+	−	+	−	−	−	+
14.8	+	+	+	−	+	+	+	+	+	+	+	(1)	+	−	−	−	+
15.8	+	+	+	−	+	+	+	+	+	+	+	(1)	+	−	−	−	+
15.9	+	−	+	−	+	+	+	+	+	+	+	(1)	+	−	−	−	+
16.4	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
16.8	+	+	+	−	+	+	+	+	+	+	+	(1)	+	−	−	−	+
18.9	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
19.5	+	−	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
19.8	+	+	+	+	+	+	+	+	+	+	+	+	+	−	−	−	+
20.5	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
21.3	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
22.3	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]23.6	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]23.7	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]24.2	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]24.8	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]25.6	+	−	+	−	+	+	+	+	+	+	+	+	+	−	−	−	+
[2]26.6	+	+	+	−	(1)	+	+	+	+	+	+	+	+	−	−	−	+
[2]26.7	+	+	(1)	−	(1)	+	+	+	+	+	+	+	+	−	−	−	+
[2]26.6	+	−	(1)	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]29.2	+	+	(1)	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]29.6	+	+	(1)	−	(1)	+	+	+	+	+	+	+	+	−	−	−	+
[2]30.4	+	+	(1)	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]33.0	+	+	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]33.1	+	−	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]35.2	+	(1)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]36.4	+	(1)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]37.6	(1, 4)	(1, 4)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]41.9	+[4]	(1, 4)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]43.6	+[4]	(1, 4)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[2]45.2	+[4]	(1, 4)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[5]67.8	(1, 4)	(1, 4)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[5]71.5	(1, 4)	(1, 4)	−	−	−	(1)	+	+	+	+	+	+	+	−	−	−	+
[5]72.5	(1, 4)	(1, 4)	−	−	−	+	+	+	+	+	+	+	+	−	−	−	+
[5]77.5	(1, 4)	(1, 4)	−	−	−	(1)	+	+	+	+	+	+	+	−	−	−	+
[5]81.0	(1, 4)	(1, 4)	−	−	−	(1)	+	+	+	+	+	+	(6)	−	−	−	+
[5]105.0	(1, 4)	(1, 4)	−	−	−	(1)	+	+	+	+	+	+	(6)	−	−	−	+

[1]Bump, indicates beginning of spine formation or bony overgrowth of spine.
[2]Transforming.
[3]Pelagic juvenile
[4]Parietal and nuchal spines fused.
[5]Benthic juvenile.
[6]Spine covered by fleshy lobe.
[7]Adjacent spines fused.
[8]Spine has become scale-covered.

characteristic of adults of *S. flavidus*, usually becomes distinct on juveniles >100 mm long.

Occurrence (Figures 7-10).—Adults of *S. flavidus* occur from San Diego, Calif., to Kodiak Island, Alaska (Miller and Lea 1972). Off Oregon they are most common on the continental shelf between 100 and 200 m (Snytko and Fadeev[7]). Data from Niska (1976) showed that 92% of the total Oregon trawl catch of *S. flavidus* from 1963 to 1971, was taken from depths of 54 to 218 m. Concentrations of adult *S. flavidus* have been found along Astoria Canyon, between lat. 46°10′ N and 46°20′ N, and also between lat. 44°30′ N and 45°

[7]Snytko, V. A., and N. S. Fadeev. 1974. Data on distribution of some species of sea perches along the Pacific coast of North America during the summer-autumn seasons. Document submitted to the Canada-USSR Meeting on Fisheries in Moscow-Batumi, USSR, November 1974, 14 p. (Transl. 3436, Can. Transl. Ser.)

TABLE 6.—Continued.

Standard length (mm)	Infraorbital							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supra-cleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
10.1	+	–	–	+	–	–	–	–	–	–	+	–	+	–	–
10.3	+	(1)	–	+	–	–	+	–	–	–	+	–	+	(1)	–
10.7	+	(1)	–	+	–	–	+	–	–	–	+	–	+	–	–
11.4	+	+	–	+	–	–	+	(1)	–	–	+	–	+	–	–
11.8	+	+	–	+	–	–	–	–	–	–	+	–	+	+	–
11.8	+	+	–	+	–	–	–	–	–	–	+	–	+	(1)	–
11.9	+	+	–	+	–	–	+	–	–	–	+	–	+	–	–
12.0	+	+	–	+	–	–	+	–	–	–	+	–	+	–	–
12.2	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.7	+	+	–	+	–	–	+	(1)	–	–	+	–	+	(1)	–
12.8	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.9	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	–
13.1	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.7	+	+	–	+	–	(1)	+	+	–	–	+	–	+	+	–
14.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
14.8	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
15.8	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	–
15.9	+	+	(1)	+	–	+	+	+	–	–	+	–	+	+	–
16.4	+	+	+	+	–	(1)	+	+	–	–	+	–	+	+	–
16.8	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
18.9	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
19.5	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
19.8	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
20.5	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	–
21.3	+	+	+	+	–	+	+	+	–	–	+	–	+	+	–
22.3	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
[2]23.6	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	–
[2]23.7	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	(1)
[2]24.2	+	+	+	+	–	+	+	+	–	–	+	+	+	+	(1)
[2]24.8	+	+	+	+	–	+	+	+	–	–	+	(1)	+	+	(1)
[2]25.6	+	+	+	+	–	+	+	+	–	–	(1)	–	+	+	+
[2]26.6	+	+	+	+	–	+	+	+	–	–	(1)	+	+	+	–
[2]26.7	+	+	+	+	–	+	+	+	–	–	(1)	+	+	+	–
[2]23.6	+	+	+	+	–	+	+	+	–	–	+	+	+	+	(1)
[2]29.2	+	+	+	+	–	+	+	+	–	–	(1)	+	+	+	(1)
[2]29.6	+	+	+	+	–	+	+	+	–	–	+	+	+	+	(1)
[2]30.4	+	+	+	+	–	(1)	+	+	–	(1)	(1)	+	+	+	+
[2]33.0	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	(1)
[2]33.1	+	+	+	+	–	+	+	+	–	(1)	+	+	+	+	(1)
[2]35.2	+	+	+	+	–	–	+	+	–	(1)	(1)	+	+	+	+
[2]36.4	+	(1)	(1)	(1)	–	–	(1)	+	–	(1)	(1)	+	+	+	+
[2]37.6	+	(1)	(1)	(1)	–	–	(1)	+	–	(1)	(1)	+	+	+	+
[3]41.9	+	(1)	(1)	(1)	–	–	+	+	–	+	–	+	+	+	+
[3]43.6	+	(1)	(1)	(1)	–	–	+	+	–	+	–	+	+	+	+
[3]45.2	+	(1)	(1)	–	–	–	–	+	–	(1)	(1)	+	+	+	+
[3]67.6	(6)	(6,7)	(6,7)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[3]71.5	(6)	(6,7)	(6,7)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[3]72.5	(6)	(6,7)	(6,7)	–	–	–	–	+	–	+	–	+	(1)	+	+[8]
[3]77.5	(6)	(6,7)	(6,7)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[3]81.0	(6)	(6,7)	(6,7)	–	–	–	–	+	–	+	–	+	–	+	+[8]
[3]105.0	(6)	(6,7)	(6,7)	–	–	–	–	+	–	+	–	+	–	+	+[8]

N (see footnote 7). Larvae, including transforming specimens, of *S. flavidus* in our collections were captured at stations ranging from 24 to 266 km offshore. Larvae apparently range widely and the limit observed are probably most indicative of sampling effort. Within the size range of identified larvae, there was no apparent distribution pattern relative to specimen size. Pelagic juveniles were similarly distributed. Benthic juveniles were taken close to the coast at depths of 20-37 m.

Adult *S. melanops* reportedly occur from Paradise Cove, Baja California, to Amchitka Island, Alaska (Miller and Lea 1972), although Quast and Hall (1972) noted that records from the Aleutian Islands may have resulted from misidentified *S. ciliatus*. *Sebastes melanops* is most common on the continental shelf at depths <200 m (Dunn and Hitz 1969; Niska 1976). Data tabulated by Niska (1976) for Oregon trawl catches show that 82% of the total *S. melanops* landings, from 1963 to 1971, were taken in depths <54 m while 93% were taken at depths <109 m. Larvae, including transforming specimens, of *S. melanops* in our collections were captured at stations ranging from 5 to 266 km offshore. Pelagic juveniles have a similar distribution. Larvae seem to range widely. However, sampling effort was not uniform over the area and relatively little sampling occurred nearshore, <40 km from

TABLE 7.—Development of spines in the head region of *Sebastes melanops* larvae and juveniles. + denotes spine present and – denotes spine absent.

Standard length (mm)	Preopercular (anterior series)					Preopercular (posterior series)					Opercular		Interopercular	Subopercular	Preocular	Supraocular	Postocular
	Parietal	Nuchal	1st	2d	3d	1st	2d	3d	4th	5th	Superior	Inferior					
10.6	+	(1)	+	–	+	+	+	+	+	–	(1)	–	(1)	–	–	–	+
11.7	+	(1)	+	–	+	+	+	+	+	(1)	(1)	–	(1)	–	–	–	+
11.9	+	(1)	+	+	+	+	+	+	+	+	(1)	–	(1)	–	–	–	+
11.9	+	(1)	+	+	+	+	+	+	+	(1)	(1)	–	(1)	–	–	–	+
12.4	+	+	+	–	+	+	+	+	+	+	(1)	–	(1)	–	–	–	+
12.8	+	+	+	–	+	+	+	+	+	+	(1)	–	(1)	–	–	–	+
12.8	+	+	+	–	+	+	+	+	+	+	(1)	–	+	–	–	–	+
12.8	+	+	+	–	+	+	+	+	+	+	+	(1)	+	–	–	–	+
13.5	+	+	+	–	+	+	+	+	+	+	+	–	+	–	–	–	+
13.6	+	+	+	–	+	+	+	+	+	+	+	–	+	–	–	–	+
13.9	+	+	+	–	+	+	+	+	+	+	+	(1)	+	–	–	–	+
14.0	+	+	+	–	+	+	+	+	+	+	+	(1)	+	–	–	–	+
14.9	+	+	+	–	+	+	+	+	+	+	+	–	+	–	–	–	+
15.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
15.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
15.7	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
15.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
16.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
16.5	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
17.2	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
17.4	+	+	+	+	+	+	+	+	+	+	+	+	+	–	–	–	+
17.4	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
17.7	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
17.7	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
18.5	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
19.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
19.2	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
19.2	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
20.7	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
20.7	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
21.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
22.9	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[2]23.2	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[2]24.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[2]24.0	+	+	+	–	+	+	+	+	+	+	+	+	+	–	–	–	+
[2]24.6	+	(1)	+	–	(1)	+	+	+	+	+	+	+	+	–	–	–	+
[2]27.9	+[3]	([1,3])	(1)	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[2]30.6	+[3]	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]33.1	+[3]	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]33.9	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]35.2	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]35.8	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+[5]	+	–	–	–	+
[4]38.2	+[3]	([1,3])	–	–	–	+	+	+	+	+	+	+[5]	+	–	–	–	+
[4]39.2	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+[5]	+	–	–	–	+
[4]40.0	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]41.0	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]43.8	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]45.3	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	+	–	–	–	+
[4]48.4	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	([1,6])	–	–	–	+
[7]52.5	([1,3])	([1,3])	–	–	–	+	+	+	+	+	+	+	([1,6])	–	–	–	+
[7]62.5	([1,3])	([1,3])	–	–	–	(1)	+	+	+	+	+	+	([1,6])	–	–	–	+
[7]67.0	([1,3])	([1,3])	–	–	–	(1)	+	+	+	+	+	+	([1,6])	–	–	–	+
[7]76.1	([1,3])	([1,3])	–	–	–	–	(1)	+	+	+	+	+	([1,6])	–	–	–	+
[7]89.4	—	—	–	–	–	–	(1)	+	+	+	+	+	([1,6])	–	–	–	+
[7]97.7	([1,3])	([1,3])	–	–	–	–	(1)	+	+	+	+	+	([1,6])	–	–	–	+
[7]100.9	–	–	–	–	–	–	(1)	+	+	+	+	+	([1,6])	–	–	–	+
[7]111.6	–	–	–	–	–	–	(1)	+	+	+	+	+	([1,6])	–	–	–	+

[1]Bump, indicates beginning of spine formation or bony overgrowth of spine.
[2]Transforming.
[3]Parietal and nuchal spines fused.
[4]Pelagic juvenile.
[5]Spine is bifid.
[6]Spine covered by fleshy lobe.
[7]Benthic juvenile.
[8]Spine has become scale-covered.
[9]Adjacent spines fused.

the coast. Benthic juveniles have been taken in estuaries, tidepools, and near the coast at depths <20 m.

Parturition times reported for *S. flavidus* are December to February off California (Phillips 1958) and March off Oregon (Westrheim 1975). Larvae 10-20 mm long were taken April through June, although most were taken in April and May. Larvae and pelagic juveniles 20-40 mm long were taken April through July, indicating some

TABLE 7.—Continued.

Standard length (mm)	Infraorbital							Nasal	Coronal	Tympanic	Pterotic	Posttemporal		Supracleithral	Cleithral
	Inferior			Superior								Superior	Inferior		
	1st	2d	3d	1st	2d	3d	4th								
10.6	+	–	–	+	–	–	+	–	–	–	+	–	+	(1)	–
11.7	+	(1)	–	+	–	–	+	(1)	–	–	+	–	+	+	–
11.9	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
11.9	+	+	–	+	–	–	+	(1)	–	–	+	–	+	+	–
12.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
12.8	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.5	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
13.6	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
13.9	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
14.0	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	–
14.9	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
15.4	+	+	–	+	–	–	+	+	–	–	+	–	+	+	–
15.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
15.7	+	+	(1)	+	–	–	+	+	–	–	+	–	+	+	–
15.9	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
16.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
16.5	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
17.2	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
17.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
17.4	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
17.7	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
17.7	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
18.5	+	+	+	+	–	–	+	+	–	–	+	–	+	+	–
19.0	+	+	+	+	–	–	+	+	–	–	+	+	+	+	–
19.2	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
19.2	+	+	+	+	–	–	+	+	–	–	+	+	+	+	–
20.7	+	+	+	+	–	(1)	+	+	–	–	+	+	+	+	–
20.7	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
21.0	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
22.9	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
[2]23.2	+	+	+	+	–	+	+	+	–	–	+	+	+	+	–
[2]24.0	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	–
[2]24.0	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	–
[2]24.6	+	+	+	+	–	+	+	+	–	(1)	(1)	+	+	+	–
[2]27.9	+	+	+	+	–	–	+	+	–	(1)	(1)	+	+	+	–
[2]30.6	+	+	+	+	–	–	+	+	–	(1)	+	+	+	+	(1)
[4]33.1	+	+	+	+	–	(1)	+	+	–	+	(1)	+	+	+	+
[4]33.9	+	(1)	(1)	+	–	–	+	+	–	(1)	(1)	+	+	+	+
[4]35.2	+	(1)	(1)	(1)	–	–	(1)	+	–	(1)	–	+	+	+	+
[4]35.8	+	(1)	(1)	(1)	–	–	+	+	–	+	–	+	+	+	+
[4]38.2	+	(1)	(1)	–	–	–	(1)	+	–	(1)	(1)	+	(1)	+	+
[4]39.2	+	(1)	(1)	–	–	–	(1)	+	–	(1)	–	+	+	+	+
[4]40.0	+	(1)	(1)	–	–	–	(1)	+	–	(1)	–	+	+	+	+
[4]41.0	+	(1)	(1)	–	–	–	(1)	+	–	(1)	(1)	+	+	+	+
[4]43.8	+	(1)	(1)	–	–	–	(1)	+	–	–	–	+	(1)	+	+
[4]45.3	+	(1)	(1)	–	–	–	–	+	–	+	–	+	–	+	+
[4]48.4	+	(1)	(1)	–	–	–	(1)	+	–	–	–	+	–	+	+
[7]52.5	(6)	(1)	(1)	–	–	–	–	+	–	–	–	+	–	+	+[8]
[7]62.5	(6)	(6,9)	(6,9)	–	–	–	–	+	–	–	–	+	–	+	+[8]
[7]67.0	(6)	(6,9)	(6,9)	–	–	–	–	+	–	(1)	–	+[8]	–	+[8]	+[8]
[7]76.1	(6)	(6,9)	(6,9)	–	–	–	–	+	–	–	–	+[8]	–	+[8]	+[8]
[7]89.4	(6)	(6,9)	(6,9)	–	–	–	–	+	–	–	–	+[8]	–	+[8]	+[8]
[7]97.0	(6)	(6,9)	(6,9)	–	–	–	–	+	–	–	–	+[8]	–	+[8]	+[8]
[7]100.9	(6)	(6,9)	(6,9)	–	–	–	–	+	–	–	–	+[8]	–	+[8]	+[8]
[7]111.8	(6)	(6,9)	(6,9)	–	–	–	–	+	–	–	–	+[8]	–	+[8]	+[8]

variability and protraction of parturition time. Benthic juveniles were taken only in June and October due to limited samples.

Parturition times reported for *S. melanops* are February to April (Hart 1973) and January off Oregon (Westrheim 1975). Larvae 10-20 mm long were taken April through May. Larvae and pelagic juveniles 20-40 mm long were taken April through June, indicating some variability in spawning time and duration. Benthic juveniles first appeared in June samples.

Comparisons.—Prior to this paper, developmental series of 10 of the 69 northeast Pacific (including Gulf of California) species of *Sebastes* had been described: *S. cortezi*, *S. crameri*, *S.* Gulf Type A, *S. helvomaculatus*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger* (Moser 1967, 1972; Moser et al. 1977; Moser and Ahlstrom 1978; Richardson and Laroche 1979). While exhibiting some similarities to larval and juvenile *S. flavidus* and *S. melanops*, the previously described develop-

mental series differ in many characters. Most apparent is the early lack of pigment and the later development of distinct pigment saddles under the dorsal fins of postflexion and pelagic juvenile *S. crameri*, *S. helvomaculatus*, *S. levis*, *S. melanostomus*, *S. paucispinis*, and *S. pinniger*. The only species described to date which has pigment along the dorsal surface under the dorsal fins in postflexion larvae and pelagic juveniles, similar to that of *S. flavidus* and *S. melanops*, is *S. jordani*. However, *S. jordani* has a very short snout to anus distance/SL ratio, 36 to 53% SL, compared with 57 to 60.3% SL and 58.0 to 61.3% SL for postflexion larvae and pelagic juveniles of *S. flavidus* and *S. melanops*, respectively. *Sebastes cortezi*, *S.* Gulf Type A, and *S. macdonaldi* are all deeper bodied than *S. flavidus* and *S. melanops*, and both *S.* Gulf Type A and *S. macdonaldi* have much longer parietal spines.

Other Oregon species which are easily confused with *S. flavidus* and *S. melanops* during larval and juvenile development are the widow rockfish, *S. entomelas*, and the blue rockfish, *S. mystinus*. However, pelagic and benthic juveniles of these species are separable based on the presence of preocular and supraocular spines, usually >15 dorsal soft rays, and usually >8 anal soft rays (see Appendix Table 1).

Sebastes mystinus is separable from the other three species at all sizes after fin formation has occurred, ≈9.0 mm, since it is the only species which usually has 16 dorsal soft rays and 9 anal soft rays. *Sebastes entomelas* and *S. mystinus* both usually have 18 pectoral rays which distinguish them from *S. melanops*, which usually has 19 rays. *Sebastes flavidus* and *S. entomelas* are the only pair of species which are not readily separated by fin counts. However, both *S. entomelas* and *S. mystinus* develop supraocular spines, which appear on specimens larger than ≈17 mm, while *S. flavidus* and *S. melanops* rarely develop supraocular spines. In addition to these characters, larvae and pelagic juveniles of *S. entomelas* and *S. mystinus* either lack or have a reduced number of melanophores at the articulations of the anal fin rays and on the ventral surface of the caudal peduncle. We have a description of the development of *S. entomelas* in preparation.

Sebastes ciliatus (from British Columbia and Alaska) and *S. serranoides* (from California) are other similar species which should be carefully considered when identifying specimens from areas where they also occur. We have not had the opportunity to observe specimens of *S. ciliatus* and cannot assess its potential for causing confusion. We have examined 20 benthic juvenile *S. serranoides*. Although the head spine pattern in *S. serranoides* is the same as in *S. flavidus* and *S. melanops*, *S. serranoides* usually has <18 pectoral rays and >8 anal soft rays which will usually separate them from *S. flavidus* and *S. melanops* (see Appendix Table 1). All of the species discussed, excluding *S. ciliatus* for which we have no information, have to some extent a concentration of melanistic pigmentation on the posterior portion of the spinous dorsal fin occurring on juveniles. *Sebastes flavidus* and *S. melanops* have the most intensely pigmented "black blotch." *Sebastes mystinus* has a more darkly pigmented spinous dorsal fin which presents little contrast from the pigment in the area of the black blotch. *Sebastes entomelas* and *S. serranoides* usually have a less distinct "blotch" with most of the pigment concentrated in a fringe along the posterior distal edge of the spinous dorsal fin membrane.

The most important characters useful in separating larval and juvenile *S. flavidus* and *S. melanops* from each other are pectoral ray number (usually 18 versus 19), lateral line pore number (usually >50 versus <50), and caudal peduncle depth/length ratio (mean values 0.73, 0.64, 0.64, 0.80 versus 0.88, 0.78, 0.74, 0.92 in postflexion larvae, transforming, pelagic juvenile, and benthic juvenile specimens, respectively). *Sebastes flavidus* taken at the same location as *S. melanops* appear to have less dense melanistic pigment. Benthic juveniles of *S. flavidus* seem to inhabit deeper waters, >20 m, while *S. melanops* inhabits estuaries, tidepools, and offshore waters <20 m. Landing data tabulated by Niska (1976) indicates a corresponding difference in "preferred" depth for adults with *S. flavidus* taken chiefly between 54 and 218 m and *S. melanops* taken mainly in water <54 m.

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APPENDIX TABLE 1.—Frequency distributions of soft fin rays, lateral line pores, diagonal scale rows below the lateral line, and gill rakers for juvenile and adult *Sebastes entomelas, S. flavidus, S. melanops, S. mystinus,* and *S. serranoides.*

Species	Side	Pectoral fin rays				Dorsal fin soft rays					Anal fin soft rays				Lateral line pores											
		17	18	19	20	13	14	15	16	17	7	8	9	10	45	46	47	48	49	50	51	52	53	54	55	56	59
Sebastes entomelas[1]	Left	1	37	2	—	—	4	31	5	—	3	35	2	—	—	—	—	—	—	—	—	4	6	16	13	1	—
	Right	1	37	2	—										—	—	—	—	—	—	—	4	4	19	12	1	—
Sebastes flavidus[2]	Left	2	47	3	—	—	30	22	—	—	5	47	—	—	—	1	—	—	1	4	6	15	10	5	5	1	—
	Right	1	48	3	—										—	—	—	—	—	3	11	12	15	3	3	2	1
Sebastes melanops[3]	Left	—	11	55	—	2	26	37	1	—	13	53	—	—	2	2	4	13	16	15	11	1	1	1	—	—	—
	Right	—	3	61	1										1	3	5	9	17	13	13	2	3	—	—	—	—
Sebastes mystinus[4]	Left	3	55	3	—	—	—	5	49	8	—	6	52	4	—	—	—	1	6	16	18	12	9	—	—	—	—
	Right	3	55	4	—										—	—	—	—	4	10	15	22	8	2	—	—	—
Sebastes serranoides[5]	Left	16	4	—	—	—	1	11	8	—	—	3	16	1	—	—	—	—	—	1	—	5	9	3	1	—	—
	Right	15	5	—	—										—	—	—	—	—	—	1	3	12	2	2	—	—

Species	Side	Diagonal scale rows below lateral line																			Gill rakers on lower bar of 1st gill arch						
		49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	23	24	25	26	27	28	29
S. entomelas	Left	—	—	—	—	—	—	—	—	—	—	1	2	4	6	12	7	5	2	1	—	—	11	21	7	1	—
	Right	—	—	—	—	—	—	—	—	—	—	1	1	6	5	13	4	7	2	1	—	—	13	22	5	—	—
S. flavidus	Left	—	—	—	—	—	—	—	—	3	12	8	10	6	1	3	—	1	—	—	—	5	14	30	3	—	—
	Right	—	—	—	—	—	—	1	—	1	6	16	9	4	2	4	—	1	—	—	—	1	15	31	4	—	—
S. melanops	Left	1	3	2	6	8	11	19	13	2	1	—	—	—	—	—	—	—	—	—	—	7	13	27	17	2	—
	Right	—	1	1	8	9	12	17	13	4	1	—	—	—	—	—	—	—	—	—	1	6	10	27	18	4	—
S. mystinus	Left	—	—	—	1	9	11	5	14	7	3	3	—	1	—	—	—	—	—	—	2	7	28	19	6	—	—
	Right	—	—	1	—	4	8	7	11	13	4	3	2	1	—	—	—	—	—	—	2	9	21	21	7	1	1
S. serranoides	Left	—	—	—	—	—	—	—	—	—	2	2	3	2	1	—	—	—	—	—	1	8	11	—	—	—	—
	Right	—	—	—	—	—	—	—	—	—	1	2	3	2	2	—	—	—	—	—	1	6	10	3	—	—	—

Species	Side	Gill rakers on upper bar of 1st gill arch					Total gill rakers on 1st gill arch								
		8	9	10	11	12	32	33	34	35	36	37	38	39	40
S. entomelas	Left	—	4	36	—	—	—	—	2	10	21	6	1	—	—
	Right	—	5	33	2	—	—	—	2	14	17	7	—	—	—
S. flavidus	Left	—	—	21	30	1	—	—	4	6	21	18	3	—	—
	Right	1	—	20	30	1	—	1	—	10	17	21	3	—	—
S. melanops	Left	—	1	13	46	6	—	—	4	10	9	21	17	5	—
	Right	—	—	20	41	5	—	—	5	10	8	21	16	5	1
S. mystinus	Left	—	3	43	15	1	1	1	7	25	15	9	3	1	—
	Right	—	2	47	11	2	1	1	8	20	17	9	4	2	—
S. serranoides	Left	—	4	16	—	—	1	3	5	11	—	—	—	—	—
	Right	—	7	13	—	—	—	4	5	10	1	—	—	—	—

[1]All *S. entomelas* were collected at lat. 44°39′ N, long. 124°44′ W off Oregon.
[2]All *S. flavidus* were collected at two locations (lat. 44°05′ N, long. 124°55′ W and lat. 45°33′N, long. 124°07′ W) off Oregon.
[3]All *S. melanops* were collected from Yaquina Bay, Oreg. (lat. 44°37′ N, long. 124°03′ W), or open coast tide pools nearby.
[4]*Sebastes mystinus* from a number of locations between Soberanes Point, Calif. (lat. 36°26′54″ N, long. 121°55′41″ W), and the mouth of the Columbia River, Oreg. (lat. 46°15′ N, long. 124°07′ W) were examined.
[5]All *S. serranoides* were collected in California between Newport Beach (lat. 33°35′ N) and San Francisco (lat. 37°50′ N).

EFFECTS OF TRAP VENTING ON GEAR SELECTIVITY IN THE INSHORE RHODE ISLAND AMERICAN LOBSTER, *HOMARUS AMERICANUS*, FISHERY

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ABSTRACT

The incorporation of escapement devices in lobster traps has proven effective in allowing the release of sublegal-sized American lobster, *Homarus americanus*, and reducing the potential for trap related injury and mortality. The present study was undertaken to assess the effects of trap venting on size selectivity and catch per unit effort in the inshore Rhode Island lobster fishery. The use of rectangular vents (42 × 152 mm) resulted in a 79% decrease in the sublegal (<78 mm carapace length) catch. Vented traps tended to consistently catch greater numbers of legal-sized (≥78 mm carapace length) lobster, possibly due to a density dependent effect. The mean size of lobster caught in vented gear was significantly greater than in control traps. An analysis of the effect of trap immersion time indicated that the catch is asymptotic with increasing soak time up to 7 set over days.

Comparisons of the effectiveness of 42 × 152 mm and 44.5 × 152 mm vents indicated that no substantial loss of legal lobster would occur and that escapement rates of sublegal lobster would be dramatically improved with the use of the larger vent size. Vented traps tended to be more efficient in releasing sublegal lobster than traps with equivalent lath spacing, supporting the use of synthetic vents. Vent orientation (horizontal versus vertical) did not affect the escapement of sublegal-sized lobster.

Attempts to adjust the size selectivity of traps to minimize the retention of sublegal-sized lobster have received increasing attention in recent years (Krouse and Thomas 1975; Krouse 1978; Pecci et al. 1978; Nulk 1978; Fair and Estrella[2]). The inverse relationship between lath spacing and the sublegal catch has long been recognized (Templeman 1939; Wilder 1945), while current efforts have been directed toward the development of more precise escapement devices, specifically escape vents of various designs.

A clear reduction in lobster mortality and injury with the use of vented traps has been demonstrated (Pecci et al. 1978); sources of trap related mortality and injury include aggressive interactions within the trap and the effects of handling by fishermen. In addition, predation on surface released sublegal lobster may contribute significantly to mortality (Krouse and Thomas 1975).

Less information is available on the effects of trap venting on the incidental catch of commercially valuable species, particularly the rock crab, *Cancer irroratus*, and the jonah crab, *C. borealis*. Krouse (1978) demonstrated the effectiveness of vents with circular openings in retaining marketable northern crabs *Cancer* spp., while permitting the egress of sublegal-sized lobster. Stasko (1975) earlier promoted the use of circular escape openings in traps modified to retain crabs and release lobster.

A research program designed to substantiate data available on trap venting and apprise local fishermen of new concepts in gear modification was initiated by the Rhode Island Division of Fish and Wildlife in April 1976. This report presents the results of field and laboratory investigations on the effects of trap venting on catch per unit effort (CPUE) and size composition of the lobster catch.

METHODS

Conventional lobster traps were purchased from commercial suppliers and distributed to eight cooperating fishermen. The fishermen participated on a voluntary basis and were chosen to represent a range of geographical areas within

[1]Rhode Island Department of Environmental Management, Division of Fish and Wildlife, 150 Fowler Street, Wickford, RI 02852.

[2]Fair, J. J., and B. Estrella. 1976. A study on the effects of sublegal escape vents on the catch in lobster traps in five coastal areas of Massachusetts. Unpubl. manuscr., 9 p. Massachusetts Division of Marine Fisheries, P.O. Box 707, Sandwich, MA 02563.

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[3]All *S. serranoides* were collected in California between Newport Beach (lat. 33°35' N) and San Francisco (lat. 37° 50' N).

Narragansett Bay and Rhode Island Sound. Five trap styles, representing the most commonly used trap types in this area, were selected for use in the study. Each fisherman was given traps of one type only.

Seven of the fishermen were provided with equal numbers of vented and nonvented traps to be arranged in trawls (strings) of alternating vented and control traps. The escape panels were constructed of 6061 gage aluminum with a 42 mm × 152 mm opening placed in the parlor section of the trap. Single parlor traps were equipped with one vent placed vertically in the end section of the parlor. Double parlor traps were equipped with two vents positioned horizontally in the sides of each parlor section.

To determine the efficiency of vented traps when compared with traps having equivalent lath spacing and to evaluate the effects of vent orientation (horizontal vs. vertical) on escapement, one of the fishermen was given traps with the following characteristics:

1) control traps (mean lath spacing 31 mm, SD = 6 mm),
2) traps with horizontal vents (42 mm × 152 mm),
3) traps with vertical vents (42 mm × 152 mm),
4) traps with one vertical lath space opened to 42 mm,
5) traps with horizontal vents (44.5 mm × 152 mm),
6) traps with vertical vents (44.5 mm × 152 mm), and
7) traps with one vertical lath space opened to 44.5 mm.

Each trap type was represented once in each trawl and trap order was randomized both within and between trawls.

The fishermen provided with experimental gear recorded the number of legal and sublegal lobster per trap haul. Additional information on fishing location, depth, bottom type, and soak time (set over days) was also recorded. Periodic sampling trips were made by personnel of the Rhode Island Division of Fish and Wildlife, Marine Fisheries Section. While on board commercial lobster boats, we recorded the number of legal and sublegal lobster per trap haul; physical condition including molt status, appendage loss, and the presence of an external egg mass on females; and carapace length (measured from the posterodorsal edge of the eye socket to the posterior margin of the carapace).

RESULTS AND DISCUSSION

Catch Per Unit Effort

Catch per trap haul (CTH) and CTH weighted by immersion time (CTHSOD) were examined for the seven fishermen provided with unmodified control traps and traps equipped with rectangular (42 × 152 mm) escape vents. A total of 18,984 lobster were obtained in 7,002 trap hauls of the experimental gear. The overall catch of sublegal-sized lobster was reduced by 79% in vented traps. Dramatic reductions in the sublegal catch were evident for each individual fisherman with one exception (Table 1). The ratio of sublegal to legal lobster was 1.375:1 in vented gear and 2.746:1 in control traps, again indicating the efficiency of vented traps in releasing sublegal lobster (Table 1). The overall mean CTH for sublegal lobster was 1.299 and 2.330 in vented and control traps, respectively (Table 2). These results support the findings of Krouse and Thomas (1975), Krouse (1978), Pecci et al. (1978), and Fair and Estrella (see footnote 2) in establishing the effectiveness of employing vented gear.

TABLE 1.—Number of legal (≥78 mm CL), sublegal and percentage of legal American lobster; ratio of sublegal to legal lobster (S/L); and the number of trap hauls (TH) in vented and nonvented gear for individual fisherman. Numbers in parentheses are totals adjusted to retain equal sample sizes. Chi-square contingency table analyses (χ_1^2) tested the hypothesis that the catch of legal and sublegal lobster is independent of trap type.

	Vented					Control					
Fisherman	Legal	Sublegal	% legal	S/L	TH	Legal	Sublegal	% legal	S/L	TH	χ_1^2
A	404	1,069	27.42	2.646	528	377	1,526	19.81	4.047	528	26.66**
B	404(401)	743(740)	35.22	1.839	768	401	1,783	18.36	4.446	765	114.44**
C	366	397	47.96	1.084	368	343	789	30.30	2.300	368	60.01**
D	392	273	58.94	0.696	335	249	431	36.61	1.730	335	66.31**
E	253(251)	505(486)	33.36	1.996	209	247	494	33.33	2.000	204	0.05 ns
F	320	729	30.50	2.278	349	243	1,947	11.09	8.012	349	184.71**
G	1,174	838	58.34	0.713	948	1,107	1,180	48.40	1.065	948	42.11**
Total	3,313 (3,308)	4,554 (4,532)	42.11	1.375	3,505	2,967	8,150	26.68	2.746	3,497	498.433**

**=$P<0.005$; ns=not significant.

TABLE 2.—Catch per unit effort of American lobster in vented and nonvented traps for individual fishermen. CTH indicates catch per trap haul; CTHSOD indicates catch per trap haul/set over day; the subscripts L and S indicate the catch of legal (≥78 mm CL) and sublegal lobster, respectively. Data are expressed in numbers of lobster.

	Vented				Control			
Fisherman	C_LTH	C_LTHSOD	C_STH	C_STHSOD	C_LTH	C_LTHSOD	C_STH	C_STHSOD
A	0.765	0.155	2.024	0.410	0.714	0.144	2.890	0.585
B	.526	.160	.967	.294	.524	.159	2.330	.709
C	.994	.141	1.078	.153	.932	.132	2.144	.305
D	1.170	.300	.814	.209	.743	.191	1.286	.330
E	1.210	.244	2.416	.487	1.211	.244	2.421	.488
F	.916	.175	2.088	.399	.696	.133	5.787	1.107
G	1.238	.251	.883	.179	1.167	.236	1.244	.236
Total	0.945	.230	1.299	.317	0.848	.207	2.330	.569

Interestingly, vented traps tended to consistently catch more legal-sized lobster than control traps (Tables 1,2). The overall mean CTH for legal lobster was 0.945 in vented traps and 0.848 in nonvented gear (Table 2). We attributed the trend in lower legal catch in control traps to a saturation effect where the probability of a lobster entering a trap declines with increasing density within the trap. In nonvented traps, sublegal lobster occupy space which might otherwise be taken by legal-sized lobster. Direct evidence of catch density dependence of this type in a trap fishery has been demonstrated for two species of *Cancer* (Miller 1979).

The well-established aggressive behavior of lobster when held in confinement supports the concept of a saturation effect for this species. Lobster are characteristically solitary under natural conditions (Cobb 1971; O'Neill and Cobb 1979) and it is reasonable to assume that the presence of lobster within a trap deters further entries. Although relatively little is known of the trap-related behavior of this species, there is an apparent conflict between food (and/or shelter) seeking behavior and avoidance of conspecifics.

Krouse (1978) reported an increase in legal catch in vented traps, supporting conclusions derived in an earlier study conducted in Maine (Krouse and Thomas 1975). Templeman (1939) and Wilder (1945) had earlier demonstrated increased legal catch rates in traps with increased lath spacing.

In the present study, the impact of crowding on the legal catch was most pronounced in small mesh (2.5 cm × 2.5 cm) wire traps (Fisherman F). These traps retained extremely high numbers of sublegals. Vented traps not only retained fewer sublegal lobster, but caught substantially more legal-sized lobster (Tables 1, 2).

To further assess the effectiveness of the vented gear, we tested the hypothesis that the catch of legal and sublegal lobster was independent of trap type (vented vs. control). In two instances where loss of trap resulted in an unequal number of observations, catch totals were adjusted by deleting data from an adjacent trap to retain a balanced design. Lost traps were replaced as quickly as possible. These analyses confirmed that significant differences exist in the catch characteristics of vented and control traps for combined data ($\chi_1^2 = 498.433$; $P<0.005$) and for individual fishermen (Table 1) with a single exception.

Effect of Immersion Time

The importance of incorporating soak time in measures of CPUE has been emphasized in several trap fisheries including that for the American lobster (Thomas 1973; Skud[3]), the European lobster, *H. gammarus* (Bennett 1974), the spiny lobster, *Panulirus argus* (Austin 1977), and the western rock lobster, *P. longipes cygnus* (Morgan[4]).

The immersion (soak) time utilized by individual fishermen is most often a function of the total number of traps deployed and the daily hauling capacity of the boat, although weather conditions frequently interrupt hauling schedules. Each fisherman typically has three or more sets of gear which are hauled in rotation.

Catch data were pooled and examined for the effect of immersion time up to a maximum of 7 set over days. Soak times of >7 days were omitted due to excessive variability. The catch of legal lobster

[3]Skud, B. E. 1976. Soak time and the catch per pot in an offshore fishery for lobsters (*Homarus americanus*). Int. Cons. Explor. Mer, Special meeting on population assessments of shellfish stocks, No. 8, 25 p.

[4]Morgan, G. R. 1976. Trap response and the measurement of effort in the fishery for the western rock lobster. Int. Cons. Explor. Mer, Special meeting on population assessments of shellfish stocks, Contrib. 16, 18 p.

per trap haul (C_LTH) tended to increase slightly with increasing soak time in both vented and control traps up to 6 days when a slight decline became evident (Figure 1).

A different pattern emerged for the catch of sublegal lobster per trap haul (C_STH) where we noted an initial increase in C_STH in nonvented traps followed by a general decline with increasing soak time. In vented traps, C_STH declined initially followed by a slight increase with time (Figure 1). The decline in C_STH in control traps with immersion times in excess of 2 days may be the result of escapement through the trap heads and mortality within the trap (Bennett 1974; Austin 1977). We attributed the immediate decline in C_STH in vented traps to escapement, indicating the effectiveness of the vents. It is unclear whether the increase in C_STH for the sixth set over day was due to sampling bias or some other factor. Bennett ascribed catch increases with long soak times to decay of the bait with an associated renewed release of chemical attractants.

The catch of legal and sublegal lobster was not proportional to immersion time. This may be due to the combined effects of declining local availability, trap saturation, escapement, and mortality (Bennett 1974; Austin 1977; Skud see footnote 3; Bennett and Brown[5]). Catch per trap haul/set over day (CTHSOD) declined with time in both vented and control traps (Figure 2). Similar observations of declining CTHSOD with increasing soak time have been noted in the Maine lobster fishery (Thomas 1973), the spiny lobster fishery (Austin 1977) and the European lobster fishery (Bennett 1974).

Our data indicated that CTH approached an asymptote with increasing soak time for both legal and sublegal lobster. Following the approach of Sinoda and Kobayasi (1969) and Munro (1974) this relationship may be modelled as:

$$C_s = C_\infty(1 - \exp(-Rs))$$

[5]Bennett, D.B., and C.G. Brown. 1976. The problems of pot immersion time in recording and analysing catch-effort data from a trap fishery. Int. Cons. Explor. Mer, Special meeting on population assessment of shellfish stocks, No. 6, 8 p.

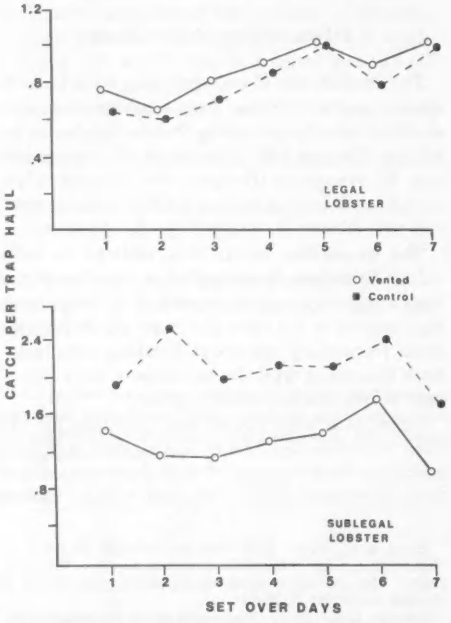

FIGURE 1.—Relationship between catch per trap haul of American lobster and trap immersion time in vented and control traps. Legal lobster are ≥78 mm CL.

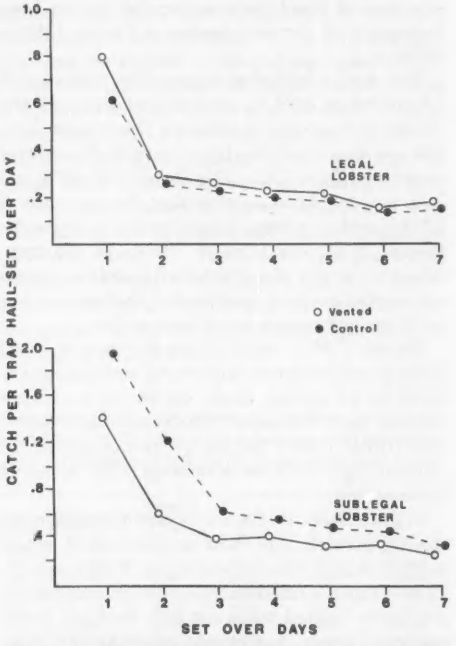

FIGURE 2.—The relationship between catch per trap haul/set over day of American lobster and trap immersion time in vented and control traps.

where C_s is the cumulative catch on day s, C_∞ is the asymptotic catch, and R is the net retention rate assuming constant availability. The term C_∞ is dependent on not only the physical holding capacity of the trap but on any behavioral interactions which serve to limit the catch. The asymptotic catch will be reached when ingress is balanced by escapement.

Parameters of the model were estimated by nonlinear least squares (Hartley 1961). The trend in greater legal catch in vented gear was reflected in the slightly higher estimate of C_∞ in vented traps (Table 3). The substantially lower asymptotic catch level for sublegal-sized lobster in vented gear clearly demonstrated the effectiveness of these traps. Munro (1974) stressed the importance of escapement in determining saturation levels in fish traps.

This model may also be used to standardize effort to a common soak time. Adapting the approach of Sinoda and Kobayasi (1969) and Caddy,[6] weighting coefficients are given by

$$\omega = \frac{1-\exp(-Rs)}{1-\exp(-Rs^*)}$$

where s^* is the standard soak time. The total effective effort (f_{tot}) is then the product of nominal effort (trap hauls) and the weighting coefficient (Caddy see footnote 6)

$$f_{tot} = \sum^{s} f_s \omega$$

and the standardized CPUE is given by the catch divided by f_{tot}. Adjustment for variable soak times should greatly improve the precision of catch effort data used in surplus yield modelling.

Size Selectivity

Carapace length (CL) measurements were obtained for a sample catch of 2,943 lobster retained in the experimental traps. The reduction in the sublegal catch retained in vented gear was most pronounced for lobster <75 mm CL (Figure 3). Size selection for lobster >75 mm CL was virtually identical in vented and control traps. The mean size of lobster caught in nonvented traps (75.20 mm) and vented gear (78.99 mm) were significantly different ($t = 12.856$; $P<0.01$).

Retention curves (Krouse and Thomas 1975) constructed for vented and control traps clearly reflect the differences in the retention characteristics for each trap type (Figure 4). The cumulative retention points for each curve at the Rhode Island minimum legal size at the time of this study (78 mm CL) were 56.0% and 69.5% for vented and control traps, respectively.

TABLE 3.—Coefficients and associated standard errors for the model $C_s = C_\infty[1-\exp(-Rs)]$ relating catch per trap haul and soak time in vented and control traps for legal- (≥78 mm CL) and sublegal-sized lobster.

Item	C_∞	R
Vented:		
Legal	0.9745±0.0715	0.9879±0.3610
Sublegal	1.3847±0.1598	0.8796±0.6289
Control:		
Legal	0.9222±0.0811	0.7428±0.2664
Sublegal	2.1642±0.1127	2.5369±1.7001

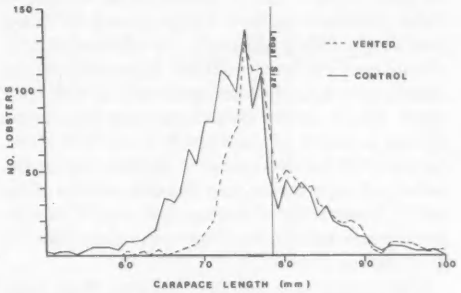

FIGURE 3.—Size-frequency distribution of American lobster collected in vented and control traps in Narragansett Bay-Rhode Island Sound (1976-77).

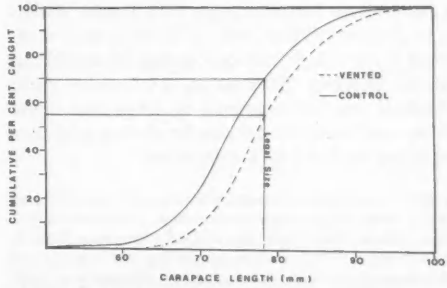

FIGURE 4.—Retention curves generated for vented and control traps for American lobster collected in Narragansett Bay-Rhode Island Sound (1976-77).

[6]Caddy, J. D. 1977. Some considerations underlying definitions of catchability and fishing effort in shellfish fisheries, and their relevance for stock assessment purposes. Int. Cons. Explor. Mer, Shellfish and Benthos Committee, C.M. 1977/K:18, 21 p.

We observed a general relationship between the mean size of lobster caught and fishing location. Comparisons of the mean size of lobster in sample catches (pooled by trap type) for six fishermen, for which adequate data were available, revealed a segregation by fishing location (Table 4). In general, lobster taken in Narragansett Bay and nearshore Rhode Island Sound samples were significantly smaller ($\alpha = 0.05$) than those taken in offshore Rhode Island Sound when compared using Duncan's multiple range procedure (Steel and Torrie 1960), although one offshore sample did not conform to this pattern. We attributed the smaller mean size in Narragansett Bay and nearshore Rhode Island Sound samples to intense fishing pressure in these easily accessible areas. Krouse (1973) noted a similar correspondence between fishing intensity and size composition of the catch. Areas within Narragansett and Rhode Island Sound with the smallest mean size of lobster also had the lowest CPUE (Table 4).

Characteristics of the habitat may also influence the size composition of the catch. Several authors have observed a correlation between the size of lobster and the size of available shelter sites (Scarratt 1968; Cobb 1971; Stewart 1972). Larger lobsters were found in areas with greater shelter size (Scarratt 1968; Cobb 1971) or in mud areas with a high clay fraction capable of supporting larger burrows (Stewart 1972). Inshore rocky habitats are characterized by ledge and mixed rocky debris which offer smaller shelter sites than offshore mud and rock substrates.

TABLE 4.—Results of Duncan's multiple range procedure comparing mean carapace length (rank ordered) of American lobster from offshore Rhode Island Sound (R.I.S.), nearshore Rhode Island Sound (R.I.S.N.) and Narragansett Bay (N.B.). Means with the same letter code are not significantly different ($\alpha = 0.05$).

Fisherman	N	Mean (SD)	Grouping	Location
C	149	78.382 (8.06)	A	R.I.S.
G	801	78.052 (7.14)	A	R.I.S.
E	107	75.738 (5.76)	B	R.I.S.
F	958	75.603 (6.44)	B	N.B.
A	71	74.845 (5.41)	B C	R.I.S.N.
B	431	73.635 (5.31)	C	N.B.

Sex Ratios

Comparisons of sex ratios in vented and control traps revealed interesting differences. We noted a female:male ratio of 1.68:1 in nonvented traps and 2.15:1 in vented gear. Contingency table analyses indicated that the sex composition of the catch differed significantly in vented and control traps ($\chi_1^2 = 7.70; P<0.01$). These data suggest differential escapement by males and females. To further assess this possibility, we investigated the relationship between carapace length and carapace width for 437 male and 603 female lobster. Analyses of covariance (Steel and Torrie 1960) indicated that the regression coefficients were significantly different ($F_{1,1036} = 6.74$; $\alpha = 0.01$). The least squares regression equations were

$$CW_m = -0.8901 + 0.6186\, CL_m \ (r = 0.869) \text{ for males and}$$
$$CW_f = -4.3932 + 0.6755\, CL_f \ (r = 0.886) \text{ for females.}$$

In passing through a rectangular vent, the critical body dimension is the carapace width (the minimum body measure). The relatively broader carapace width for females of a given carapace length may result in the retention of proportionately more females, accounting for the observed discrepancy in sex ratios in the experimental gear. It should be noted that Krouse and Thomas (1975) found no significant differences in the carapace width-length relationship for 114 female and 103 male lobster.

Vent Size, Orientation, and Lath Spacing

We examined the effect of vent orientation (horizontal vs. vertical) and lath spacing on escapement. The effectiveness of larger vents (44.5 mm × 152 mm) in retaining legal lobster was also tested. Vent orientation may affect either the probability of a lobster locating the vent or the time required to find the vent, a factor of importance with short immersion times. There may also be differences in size selectivity associated with vent orientation. Analysis of preliminary size composition data indicated that 42 mm vents may in fact be too small for a minimum legal size of 78 mm. Accordingly, we tested 44.5 mm × 152 mm vents in an attempt to determine if legal-sized lobster could escape with the use of this larger vent size. We also evaluated the effectiveness of opening lath spacing to 42 mm and 44.5 mm in comparisons with vents of equivalent size.

A total of 4,487 lobster were obtained in 2,222 trap hauls of the experimental gear. As might be expected, traps with 44.5 mm openings (vented and lath spaced traps) retained markedly fewer sublegal lobster than either traps with 42 mm

openings or control traps (Table 5). The sublegal catch was substantially reduced in comparisons of traps with 42 mm escapement openings and control traps (Table 5). Contingency table analyses indicated that the catch characteristics of each vented trap type were significantly different from control traps (Table 5). Traps with horizontal vents (both size classes) tended to catch fewer legal-sized lobster than control traps (Table 5). We were unable to offer a direct explanation for this observation since, based on morphometric studies and laboratory observations, escapement of lobster ≥78 mm CL through 42 mm vents would be impossible and escapement of legal-sized lobster through 44.5 mm vents would be minimal. The effect of vent orientation on the sublegal catch was negligible. Krouse (1978) found no significant differences in the catch characteristics of traps equipped with horizontal and vertical vents.

Traps with increased lath spacing tended to retain more sublegals than traps equipped with equivalent-sized vents (Table 5) suggesting that synthetic vents were more efficient escapement devices. In this experiment the opened lath spacing was oriented vertically in the end panel of the parlor section of the trap. Although the vent width determines the selection characteristics of the trap, the length and orientation of the vent (or lath spacing) may directly affect the probability of locating the opening. Vertically positioned escape openings offer a target equal to the width of the opening, a relatively small area while horizontally positioned vents proffer a much larger target. Laboratory observations indicated that escapement openings were located by an apparently random search process, suggesting that larger target areas will be located more quickly and efficiently.

The catch of legal-sized lobster tended to increase slightly or remain constant with increasing soak time for each trap type with the exception of control traps, which demonstrated a decline as immersion time increased (Figures 5, 6). The catch of sublegal lobster remained consistently low with increasing soak time in traps with 44.5 mm escapement openings while that for traps with 42 mm openings exhibited considerable variability (Figures 5, 6).

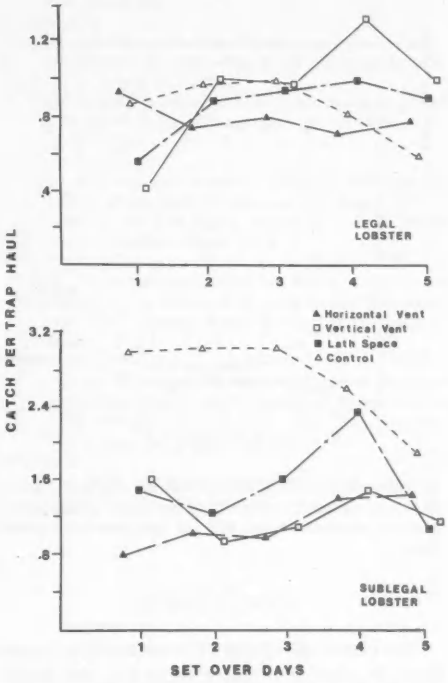

FIGURE 5.—Relationship between catch per trap haul of American lobster and trap immersion time in 42 mm vertical vented, 42 mm horizontal vented, 42 mm lath spaced, and control traps.

TABLE 5.—Number of legal (≥78 mm CL), sublegal, and percentage of legal American lobster; and ratio of sublegal to legal lobsters (S/L) and catch per unit effort in experimental traps. CTH and CTHSOD denote catch per trap haul and catch per trap haul/set over day, respectively. The subscripts L and S indicate the catch of legal and sublegal lobster. The abbreviations V, H, and L refer to vertical and horizontal vent orientation and lath spacing. Numbers in parentheses are totals adjusted to retain equal sample sizes. Chi-square contingency table analyses compared the catch characteristics of control traps with each individual trap type.

Vent type	Legal	Sublegal	% Legal	S/L	TH	C_LTH	C_LTHSOD	C_STH	C_STHSOD	χ_1^2
Control	296(292)	913(904)	24.48	3.084	316	0.936	0.436	2.889	1.068	
V 42 mm	318(315)	369(360)	46.28	1.160	318	1.000	0.369	1.160	.429	96.44**
H 42 mm	245(243)	357(352)	40.69	1.457	319	.768	0.284	1.119	.414	50.39**
L 42 mm	282(278)	454(442)	38.31	1.609	318	.886	0.328	1.427	.528	42.66**
V 44.5 mm	288(284)	136(132)	67.92	.472	318	.905	0.335	.427	.158	256.58**
H 44.5 mm	265(265)	112(111)	70.29	.422	318	.833	0.307	.352	.130	263.31**
L 44.5 mm	299	153	66.15	.511	313	.955	0.353	.488	.180	246.80**

**$P<0.005$.

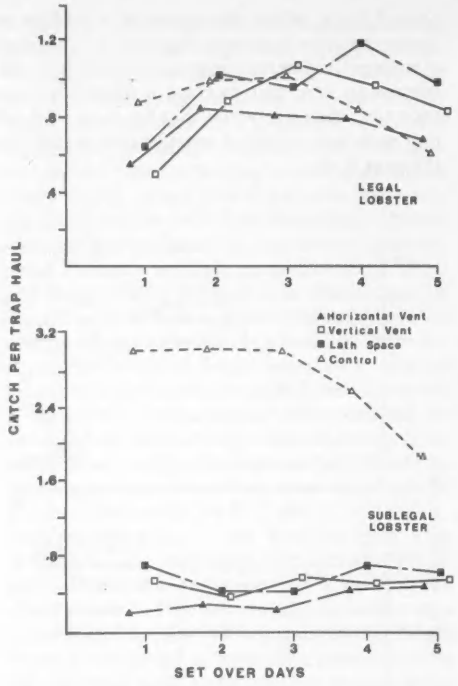

FIGURE 6.—Relationship between catch per trap haul of American lobster and trap immersion time in 44.5 mm vertical vented, 44.5 mm horizontal vented, 44.5 mm lath spaced, and control traps.

CONCLUSIONS

The beneficial effects of incorporating escape vents in standard lobster traps are well established (Krouse and Thomas 1975; Krouse 1978; Pecci et al. 1978). A reduction in lobster injury and mortality and a reduction in onboard sorting time are among the benefits accrued through the use of escapement devices (Krouse and Thomas 1975; Pecci et al. 1978). Lobster damage is related to the effects of fishing activity both directly as a result of handling (Scarratt 1973; Krouse 1976) and indirectly as a result of aggressive encounters in the trap (Pecci et al. 1978). Although interspecific aggression levels are relatively low under natural conditions (Cooper and Uzmann 1977), the artificially close confines of a trap may increase the probability of aggressive behavior.

The results of the present study confirm the utility of employing escapement devices in lobster traps. We noted substantial reductions in the catch of sublegal-sized lobster, reducing the probability of injury and mortality. Vented traps tended to consistently capture more legal-sized lobster than control traps. We attributed this increase to an inverse relationship betweeen density in the trap and the probability of new entries.

This apparent increase in relative gear efficiency may have a significant impact on catch rates if widely applied and should be closely monitored. Given the critically high levels of fishing mortality for lobster in virtually all sectors, this increase in trap fishing power is presently inadvisable. The use of 100% retention of legal-sized lobster as the primary criterion for the establishment of escape vent dimensions should therefore be modified to allow for some minimal escapement of legal lobster and to maximize escapement of sublegal lobster.

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ACOUSTIC MEASUREMENTS OF A MIGRATING LAYER OF THE MEXICAN LAMPFISH, *TRIPHOTURUS MEXICANUS*, AT 102 KILOHERTZ

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ABSTRACT

Biological sampling in a migrating scattering layer recorded at 102 kilohertz resulted in collections which consisted primarily of juvenile *Triphoturus mexicanus*. The scattering from this layer was quantified. Volume scattering strengths and corresponding target strengths were determined. The rate of migration and the target strength of *T. mexicanus* changed as the layer approached the surface. Target strengths at 102 kilohertz ranged from −60.6 decibels at 284 m to −71.3 decibels at 206 m.

Initial investigations of the deep scattering layer (DSL) emphasized military and hydrographic applications and used relatively low-frequency echo sounders (20-80 kHz). Later, research was directed at the biological organisms responsible for sound scattering in the DSL but was still confined largely to low-frequency studies. Fishes and physonectid siphonophores have been identified as the major scatterers in this frequency range (Barham 1963). In addition to determining the sources of scattering, oceanographers, fishery biologists, and commercial fishermen have been using acoustics to locate and quantify fish schools and shoals. Quantitative studies require the measurement of volume scattering strengths from the water column and knowing (or measuring) the ability of the fishes to scatter sound (acoustic cross section or target strength). Recent compilations of work in these areas can be found in Farquhar (1970) and Andersen and Zahuranec (1977).

The development of high-frequency echo sounders (>50 kHz) during the past 10 yr has progressed to the point where research at frequencies up to 3.0 MHz is now practical (Holliday and Pieper[2]). Working with high frequencies has several advantages over low frequencies. As the frequency is increased, shorter pulses can be used and the resolution is increased. In addition, smaller organisms become better sound scatterers as the frequency is increased. At 102 kHz, for example, shoals of euphausiid shrimp can be detected and quantified at ranges up to 300 m (Bary and Pieper 1970; Pieper 1979).

The present paper reports on two migrating scattering layers recorded only at 12 kHz and a deeper, third layer recorded at both 12 kHz and 102 kHz. Large numbers of a single size class of juvenile Mexican lampfish, *Triphoturus mexicanus* (Gilbert 1890), were collected from the deepest scattering layer. Volume scattering strengths of this layer were measured at 102 kHz and corresponding target strengths of *T. mexicanus* were calculated. Although no directed sampling was completed in the two, shallower, 12 kHz scattering layers, the possible scatterers responsible for these layers are indicated. We discuss the advantage of using acoustic frequencies above swim bladder resonance for biomass studies and recommend the increased usage of high-frequency acoustics for biological studies in the sea.

METHODS

Three 12 kHz scattering layers were observed migrating towards the surface near sunset on an acoustic survey at the northwest end of the San Clemente basin off southern California on 25 and 26 January 1977. The deepest of these 12 kHz layers was recorded as a strong scattering layer on a 102 kHz echo sounder being used to study euphausiid distributions (Pieper 1979). Quantitative acoustic measurements at 102 kHz and biological sampling were completed in this scattering layer on 26 January. Salinity and temperature profiles were taken immediately after the tow

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[2]Holliday, D. V., and R. E. Pieper. 1978. Volume scattering strengths and zooplankton distributions at acoustic frequencies between 0.5 and 3 MHz. Program of the 96th Meeting of the Acoustical Society of America, Honolulu, Hawaii, 25 p.

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with a submersible salinity, temperature, and depth (STD) recorder.

Acoustic Measurements

A Ross Laboratories[3] 102 kHz echo sounder with its transducer housed in an Endeco V-fin was used in conjunction with a 12 kHz hull mounted Edo transducer triggered by an Edo model 444 transceiver and model 551 recorder. Information from the 12 kHz sounder was recorded only as qualitative echograms. Acoustic data from the 102 kHz echo sounder was recorded qualitatively as echograms, and quantitatively over specific 20 m (26.87 ms) intervals where the scattering was observed. The returned signal for this interval was electronically squared and integrated for each pulse, and the value displayed on a chart recorder. The average scattering level (RL) over this 20 m interval was then calculated and the volume scattering strength (S_v) was determined by the following (Urick 1975):

$$S_v\,(\mathrm{dB/m^3}) = RL - SL + 40\log r + 2\alpha r - 10\log V$$

where RL = average received (scattering) level
SL = source level
r = mean range of the 20 m interval
α = absoprtion loss per m^3
V = volume insonified = $(c\tau/2)(\Psi r^2)$
where c = speed of sound
τ = pulse length
Ψ = solid angle of the ideal two-way beam pattern.

Volume scattering strengths were determined at various times (and depths) as the layer migrated toward the surface.

Biological Sampling

Biological samples were collected with a 6-ft modified Tucker trawl with an acoustically controlled opening-closing sequence and a continuous depth readout on a Gifft recorder. While sampling in the migrating scattering layer, the net depth was regulated to keep pace with the movement of the layer. The samples were preserved in 10% buffered Formalin in the field and transferred to 70% ethanol in the laboratory. All fishes were identified to species and their standard length measured.

The density of fishes collected was calculated by dividing the number of animals caught by the product of ship speed (meters per minute) times the length of the tow (minutes) times the mouth area (square meters). The mouth area of the net has been calculated to be 2.36 m^2 assuming a 45° fishing angle (Davies and Barham 1969).

Swim bladders were measured from 12 *T. mexicanus* which represented the range of sizes of this species collected by the trawl in the 102 kHz scattering layer (trawl 25660[4]). Swim bladder measurements were also taken from four *Protomyctophum crockeri*, five *Argyropelecus sladeni*, and five *Vinciguerria lucetia* collected from two earlier trawls (trawls 25657 and 25658). The volume of the swim bladder was calculated by using the formula for a prolate spheroid (Capen[5]).

Calculations

The density of fishes was then used to calculate their average target strength (TS) by applying the formula:

$$TS = S_v\,(\text{fishes}) - 10\log\,(\text{fishes m}^{-3})$$

where S_v (fishes) = $10\log[\log^{-1} 0.1\,S_v\,(\text{total}) - \log^{-1} 0.1\,S_v\,(\text{plankton})]$.

The S_v value for plankton was calculated from an average of the two integration values recorded after the fish scattering layer had migrated out of the integration window.

The depth where the swim bladder would resonate at 12 kHz was calculated for the range of swim bladder sizes observed assuming constant swim bladder volume with depth. These calculations were determined by solving for z (depth) in the following simplified formula for resonance of an air bubble in water (Clay and Medwin 1977; equation 6.3.10):

$$f_{FR} = (3.25 \times 10^6/a)(1 + 0.1z)^{1/2}$$

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]All trawl numbers mentioned refer to ship's station numbers (*Velero IV*, University of Southern California).

[5]Capen, R. L. 1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electronics Laboratory, San Diego, Calif., Rep. 1447, 25 p.

where f_{FR} = resonant frequency (Hz)
a = equivalent spherical radius (μm)
z = depth (m).

In the above formula, f_{FR} is 12 kHz. The a is the radius of a sphere equal in volume to that of the swim bladder at the surface.

RESULTS

The deepest of the three 12 kHz scattering layers (Figure 1) was also recorded at 102 kHz (Figure 2). The calculated volume scattering strengths at 102 kHz and at different times and depths are also shown in Figure 2. The biological sample from this layer was composed almost exclusively of juvenile *T. mexicanus* (Table 1). The movement of the scattering layer with time showed an increasing rate of migration up to a depth of around 180 m which corresponded to a change in the temperature-salinity characteristics of the water (Figure 3).

Calculated target strengths for *T. mexicanus* (Table 2) were highest at the deepest depth (−60.6 dB at 284 m) and slowly decreased as the layer migrated upwards (−71.3 dB at 206 m). The decrease in calculated target strengths corresponded to the increased migratory rate of the layer (Fig-

TABLE 1.—Biological collection from trawl 25660 taken in the 102 kHz scattering layer of San Clemente basin, southern California, 26 January 1977, 1731-1744 h.

Taxon	Total number caught	Number per 1,000 m³	Mean standard length (mm)	SE
Triphoturus mexicanus	263	114.0	24.5	0.2
Stenobrachius leucopsarus	3	1.3	24.7	1.4
Lampanyctus ritteri	1	0.4	68.5	
Argyropelecus sladeni	2	0.9	10.5	3.0
Sergestids	9	3.9	26.7	2.9
Euphausiids	105	45.0	17.4	0.7

TABLE 2.—Volume scattering strengths (S_v) for the 102 kHz scattering layer and calculated target strengths (TS) for *Triphoturus mexicanus*. Data from San Clemente basin, southern California, 26 January 1977.

Time (PST)	Type of scattering	Depth (m)	S_V (dB/m³)	Fish S_V (dB/m³)	Fish TS (dB)
1719.0	Plankton	257	−76.86	—	—
1735.0	Plankton	244	−77.31	—	—
	Average plankton	—	−77.08	—	—
1716.0	Plankton and fish	284	−69.13	−70.02	−60.6
1726.0	Plankton and fish	257	−71.13	−72.40	−63.0
1726.5	Plankton and fish	257	−71.13	−72.40	−63.0
1730.5	Plankton and fish	244	−72.83	−74.88	−65.4
1731.0	Plankton and fish	244	−73.05	−75.24	−65.8
1736.0	Plankton and fish	226	−74.48	−77.94	−68.5
1736.5	Plankton and fish	226	−74.18	−77.30	−67.9
1740.5	Plankton and fish	206	−75.23	−79.83	−70.4
1741.0	Plankton and fish	206	−75.53	−80.76	−71.3

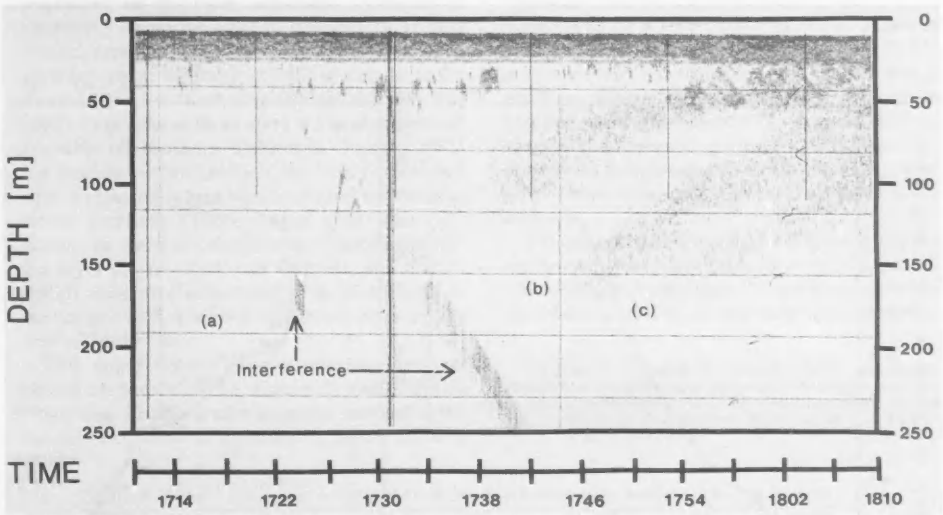

FIGURE 1.—A 12 kHz echogram from the San Clemente basin, southern California, 26 January 1977. Three scattering layers are shown, first appearing at depths around 150 m, and then migrating towards the surface. The first two scattering layers, (a) and (b), to migrate (starting around 1720 and 1745, respectively) were only recorded at 12 kHz. The third scattering layer (c) (starting around 1750) was also recorded on a 102 kHz echo sounder. The echogram also shows scattering from single fish or small fish schools between 50 m and the surface. The interference indicated is from the ship's echo sounder.

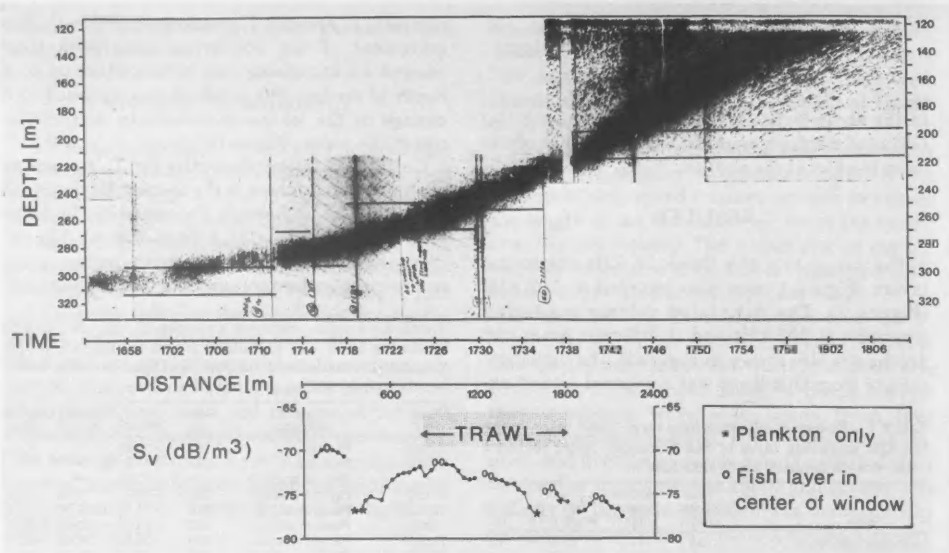

FIGURE 2.—A qualitative 102 kHz echogram showing a migrating scattering layer in San Clemente basin, southern California, 26 January 1977, and calculated volume scattering strengths (S_v) at 102 kHz for selected 20 m depth intervals (horizontal solid lines on echogram). The volume scattering strengths are shown when the scattering layer is in the center of the integration window (open circle), partially in the window (solid circle), and absent from the window (asterisk). The towing period for trawl 25660 is shown.

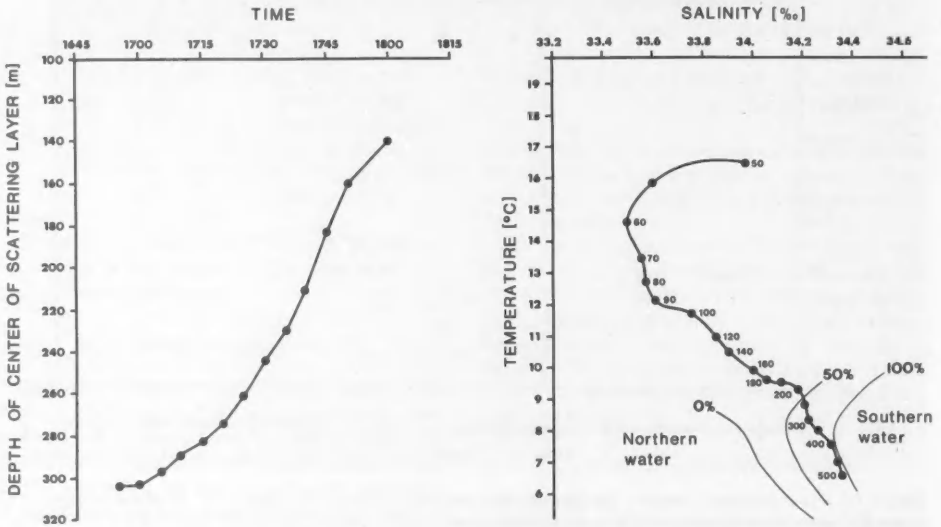

FIGURE 3.—Left: Depth of the center of the 102 kHz scattering layer plotted against time. Right: The temperature-salinity diagram for the water column immediately after trawl 25660.

ure 4). Measurements were not taken <206 m due to increased interference from surface scattering.

The organisms which were responsible for producing the two, shallower, 12 kHz scattering layers are not known since no trawls were taken from the depths of these two layers. Before the migratory period, however, two trawls were completed from depths which might correspond to the distributions of the scattering organisms. Trawls 25657 (1350-1432 h; 292-302 m) and 25658 (1514-1547 h; 267-268 m) were completed before the scattering layers became evident on either echo sounder. They were also from shallower depths than the first appearance of the 102 kHz scattering layer (1638; 315-325 m). Data from these trawls consisted of small numbers of *Argyropelecus sladeni*, *Cyclothone signata*, *Protomyctophum crockeri*, and *Vinciguerria lucetia* (Table 3). Of these four species, only *C. signata* is known not to be a vertical migrator (Rainwater 1975; Pearcy et al. 1977). Swim bladder resonance calculations for the other three species are shown in Table 4.

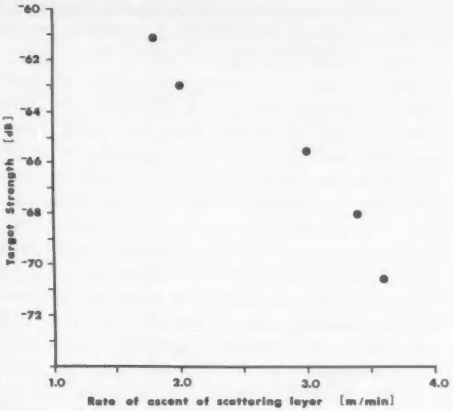

FIGURE 4.—Variations in the calculated target strengths for *Triphoturus mexicanus* at 102 kHz as a function of the rate of ascent of the 102 kHz scattering layer.

DISCUSSION

Lanternfishes (Family Myctophidae) have been implicated as the most important scatterers of scattering layers recorded at frequencies around 12 kHz, especially since many of these fishes have air-filled swim bladders of such a size as to be resonant from 1 to 30 kHz (Hersey and Backus 1962). *Triphoturus mexicanus* is a known vertical migrator off southern California (Paxton 1967) and its distribution has been previously correlated with scattering layers which showed diel migrations. Barham (1966) noted that adult *T. mexicanus* were associated with a 12 kHz scattering layer in the California Current, and Holton (1969) correlated collections of 8-10 cm long *T. mexicanus* with a strong scattering layer in the Gulf of California.

This paper reports on a scattering layer recorded at both 12 kHz (Figure 1) and 102 kHz (Figure 2). *Triphoturus mexicanus* dominated the net collection from this scattering layer (Table 1). Kleckner and Gibbs[6] suggested that lanternfishes probably regulate the gas in their swim bladders during migration to maintain constant gas volume. Assuming that calculations of swim bladder resonance can be approximated by using equations based on a free bubble in water (Hawkins 1977; Love 1978), these fish would show 12 kHz resonance only between 28 and 43 m (Table 4). In addition, a frequency of 102 kHz is too high for possible resonance effects. We suggest that the deepest 12 kHz layer and the 102 kHz layer were due to a large number of *T. mexicanus* rather than a few fishes scattering the sound at resonant frequencies.

Volume scattering strengths (Figure 2, Table 2) and target strengths (Table 2) were calculated at 102 kHz for *T. mexicanus*. Target strength values decreased as the layer migrated upwards from a

[6]Kleckner, R. C., and R. H. Gibbs, Jr. 1972. Swimbladder structure of Mediterranean midwater fishes and a method of comparing swimbladder data with acoustic profiles. Mediterranean Biological Studies Final Report to the U.S. Office of Naval Research 1(4):230-281.

TABLE 3.—Fishes collected from trawls 25657 and 25658, San Clemente basin, southern California, 26 January 1977.

Species	Trawl 25657, 1350-1432 h, 292-302 m			Trawl 25658, 1514-1547 h, 267-268 m		
	Total number caught	Number per 1,000 m^3	Mean standard length (mm)	Total number caught	Number per 1,000 m^3	Mean standard length (mm)
Argyropelecus sladeni	4	0.4	11.2	12	16.0	12.6
Cyclothone signata	10	0.9	16.6	5	6.5	16.5
Protomyctophum crockeri	5	0.5	22.9	1	1.3	12.5
Vinciguerria lucetia	3	0.3	24.0	4	5.2	23.2

TABLE 4.—Swim bladder size and calculated depths for 12 kHz resonance, assuming regulation of swim bladder volume for the specimens of *Triphoturus mexicanus*, *Protomyctophum crockeri*, *Argyropelecus sladeni*, and *Vinciguerria lucetia* in our collections.

Species	Standard length (mm)	Swim bladder				Depth[1] (m)
		Major axis (mm)	Minor axis (mm)	Volume (mm^3)	Equivalent spherical radius (μm)	
T. mexicanus	19	1.92	1.00	1.01	622	43
trawl 25660	21	1.83	.92	.81	578	36
	22	2.08	1.00	.96	612	41
	23	2.09	.95	.99	618	42
	24	1.77	.95	.84	585	37
	25	1.96	.89	.81	578	36
	25	2.03	.82	.71	553	32
	27	1.65	.89	.68	546	31
	27	1.58	.83	.57	514	26
	29	2.08	.75	.61	526	28
	33	2.08	.67	.49	⅔ fat invested	—
	39	1.50	.67	.35	Completely fat invested	—
P. crockeri	14	1.60	1.12	1.01	622	43
trawl 25657	22	1.92	1.28	1.68	738	54
	26	2.24	1.28	1.95	775	72
	29	2.24	1.44	2.25	813	80
A. sladeni	11	1.12	.64	.24	385	10
trawl 25658	14	1.28	.80	.43	468	20
	15	1.28	.80	.43	468	20
	24	2.40	1.44	2.60	853	89
	29	3.36	1.92	5.83	1,117	160
V. lucetia	21	3.16	.85	1.20	659	49
trawl 25657	22	3.54	.92	1.56	719	60
and 25658	24	3.80	.89	1.58	723	61
	26	3.86	1.14	2.63	856	90
	27	5.38	1.58	7.03	1,188	182

[1]Where swim bladder would resonate at 12 kHz, assuming constant volume at all depths.

high value of −60.6 dB at 284 m to a low value of −71.3 dB at 206 m.

The change in calculated target strength with depth could be due to two factors: either the density of fishes per cubic meter decreased with time or the target strength decreased due to the changing orientation of the migrating fishes. The second explanation is more likely for two reasons. First, the thickness of the scattering layer appears to be constant over the period where target strengths were calculated (1716-1741 h, Figure 2). Second, the increase in the migratory rate of the layer over time (Figures 2, 3) implies a more rapid, upward swimming of the fishes. This would result in a more vertical orientation of the fish in the water column.

The calculated target strengths for the juvenile *T. mexicanus* at 102 kHz (Table 2, Figure 4) can only be compared with theoretical values since no measured values could be found in the literature. Love (1977) presented formulas for predicting the target strength of an individual fish at any aspect as a function of fish size and insonifying frequency. His equations are valid for the range $1 \leq L/\lambda \leq 100$ where L is the fish length and λ is the acoustic wavelength. Our data on *T. mexicanus* for a mean standard length of 24.5 mm (Table 1) and at a frequency of 102 kHz would show a L/λ ratio of 1.7. Using his formulas on our data, calculated target strengths for dorsal aspect vary from −55.6 dB to −56.6 dB and for anterior aspect from −67.1 dB to −67.7 dB. Thus, the target strength would be decreased by 10 to 12 dB as the orientation of the fish changed from dorsal aspect to anterior aspect. The change in target strength values from our data (10.7 dB) indicates that such a change in the orientation of the fish might have occurred.

The absolute values of our calculated target strengths are about 4.5 dB less than the predicted values. Since the data used by Love (1977) to determine his equations did not include myctophids, it is possible that juvenile *T. mexicanus* (and lanternfishes in general) may be poorer scatterers than the larger, nearshore, and surface fishes used for his study.

The migratory pattern shown for this layer is not unique to this study. The increased migratory rate of scattering layers during the middle of the sunset migration has been shown by a number of authors (e.g., Kampa and Boden 1954). Kampa and Boden (1954) also correlated this type of migratory pattern to a similar pattern in the isolume at the scattering layer depths. The interrelationship between isolumes, scattering layer migrations, and vertical water mass structure is not well understood. Thus, the observed change in mi-

gratory rate with change in water type around 180 m (Figure 3) may or may not reflect the reason for the observed migratory pattern.

The scatterers responsible for the two, shallower, 12 kHz scattering layers cannot be specifically determined in the present study. Of the fishes collected from two previous tows (Table 3) only *Cyclothone signata* is known not to migrate into surface waters (Pearcy et al. 1977). Since *Vinciguerria lucetia* has been collected at the surface at night, it is probably a vertical migrator (Grey 1964). The information on the vertical distribution and migration for *Argyropelecus sladeni* and *Protomyctophum crockeri* indicates that vertical migration is unlikely, but the data on these two species are sparse and incomplete. *Argyropelecus sladeni* has been collected both day and night at depths from 0 to 2,000 m (Baird 1971; Rainwater 1975; Pearcy et al. 1977), although the center of their distribution appears to be from 100 to 500 m. The information on *P. crockeri* shows similar broad distributions (Paxton 1967; Rainwater 1975; Pearcy et al. 1977), although Paxton stated that they only reach depths of 150 m at night and Wisner[7] stated that they are not caught above 100 m at night.

Since the two, shallower, 12 kHz scattering layers were not recorded on the 102 kHz echo sounder, it is likely that swim bladder resonance at 12 kHz from a small number of organisms was responsible for the scattering. Based on swim bladder measurements made at the surface and assuming regulation of swim bladder volume to maintain constant volume during migration, the depths where 12 kHz resonance would occur were calculated (Table 4) for the range of sizes of the fishes collected. These calculations indicate that *A. sladeni* and *V. lucetia* would show 12 kHz resonance at depths from 10 to 160 m and 49 to 182 m, respectively. Thus, we suggest that one or both fishes could be responsible for the shallower, 12 kHz scattering layers. The depth range for 12 kHz resonance for *P. crockeri* (43-80 m) indicates that it was probably not the source of either of the scattering layers. In addition, both shallow layers reached a depth of 40-50 m during the migration and *P. crockeri* has not been collected at depths <100 m at night (Paxton 1967; Wisner see footnote 7). It is also possible, however, that the shallower layers resulted from an organism or organisms not collected by the two net tows discussed.

The potential use of high-frequency acoustics for studying the distribution, behavior, and abundance of scattering organisms is strongly indicated. Echo sounders operated at frequencies above 30 kHz are working at frequencies above swim bladder resonance and therefore, reflect the biomass of scatterers more accurately. In addition, they generally have narrow beam angles and utilize short pulse lengths (3.5° beam angle and 1.0 ms pulse length in this study) which produce finer resolution in the scattering patterns. Calibrated, multifrequency acoustic systems used in conjunction with sophisticated net systems are needed to better define distributional patterns and interactions of these midwater organisms.

SUMMARY AND CONCLUSIONS

Triphoturus mexicanus is known to migrate vertically in the water column (Paxton 1967). We have shown that juvenile *T. mexicanus* were the major sound scatterers in a migrating scattering layer recorded at both 102 kHz and 12 kHz. Calculated target strengths for *T. mexicanus* at 102 kHz varied from −60.6 dB at 284 m to −71.3 dB at 206 m. This decrease in target strength with depth was probably due to a change in the orientation of the fish in the water column. The lowest target strength (−71.3 dB) occurred when the scattering layer was migrating towards the surface at its highest rate and, therefore, the fishes should be oriented more vertically in the water column.

Two, shallower, scattering layers were recorded at 12 kHz but not 102 kHz. We suggest that these two layers probably resulted from scattering which occurred from fishes with swim bladders which 1) resonated at 12 kHz and 2) were regulated to maintain constant swim bladder volume during migration. *Vinciguerria lucetia* and *A. sladeni* are both possible scatterers of these layers although *A. sladeni* is not known to be a vertical migrator.

The importance of using acoustics to study mesopelagic organisms is indicated. Echo sounders can be used to both qualitatively direct biological sampling and quantitatively determine distributions and biomass. High-frequency echo sounders (e.g., 102 kHz in this study) have an advantage over low-frequency echo sounders. Target strength measurements on the midwater fishes, however, are needed to better predict the

[7]Wisner, R. L. 1976. The taxonomy and distribution of lanternfishes (Family Myctophidae) of the eastern Pacific Ocean. Navy Ocean Research and Development Activity, Bay St. Louis, Miss., Rep. 3, 229 p.

concentration of such fishes by the acoustic technique.

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EMBRYONIC DEVELOPMENT OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*, AND A FISH EMBRYO AGE ESTIMATION METHOD

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ABSTRACT

Eggs of Atlantic menhaden, *Brevoortia tyrannus*, were artificially fertilized and embryos were reared in the laboratory at 12 temperature-salinity combinations (temperature: 10°, 15°, 20°, and 25° C; salinity: 10, 20, 30‰). Salinity between 10 and 30‰ had no significant effect on embryonic mortality and no noticeable effect on rate of development. Temperature had a significant effect on embryonic mortality and rate of development. Embryonic mortality was significantly greater at 10° C than at 15°, 20°, and 25° C, and significantly greater before than after blastopore closure at 15°, 20°, and 25° C. The temperature coefficient for embryonic development of *B. tyrannus* from fertilization to hatching at temperatures between 10° and 25° C is 3.89.

Age of *B. tyrannus* embryos can be estimated by the regression of age on developmental stages when incubated at constant temperature.

The Atlantic menhaden, *Brevoortia tyrannus*, is an important commerical and forage fish of the east coast of North America (geographic range: lat. 27°-46° N). Atlantic menhaden spawn in Continental Shelf waters and in bays and estuaries in the northern part of its range during a northward spring and southward fall-winter migration (Reintjes 1961, 1969; Higham and Nicholson 1964; Kendall and Reintjes 1975; Chapoton[2]). *Brevoortia tyrannus* embryos were first described by Kuntz and Radcliffe (1917), and *B. tyrannus* embryos captured at sea have been reared in the laboratory by Reintjes (1968) and Hettler (1970), but rearing conditions were not well controlled and details on development were not published.

Rapid growth and low natural survival characterize the early life history of many marine fishes. Presented in this paper are results of a laboratory experiment to determine effects of temperatures between 10° and 25° C and salinities between 10 and 30‰ on survival and development rates of *B. tyrannus* embryos. Also presented is a useful method for estimating fish embryo age from empirical relations between embryo age, stage of development, and temperature. This fish embryo age estimation method is simple and has broader practical applications than other methods. It was developed for use in ichthyoplankton research to identify cohorts, construct embryonic stage life tables, and back calculate the time of day of spawning.

MATERIALS AND METHODS

Adult Atlantic menhaden were captured by gill nets off the Shoreham Power Plant, Long Island, N.Y., at 2300 h on 14 June 1973 (lat. 40°58′ N, long. 72°52′ W; water temperature 20.5° C; salinity 23.5‰). Eggs from a sexually mature female *B. tyrannus* were artificially fertilized on shipboard with milt from five adult males. Fertilized eggs were carried in four 1 l glass jars in an insulated box to the laboratory at the Marine Sciences Research Center, State University of New York at Stony Brook, N.Y.

Laboratory rearing experiments were two-factor, 4 × 3 (temperature × salinity) factorial designs with two replicates per treatment. Twenty-five embryos were transferred to each culture dish containing 85 ml water with salinities 10, 20, or 30‰, and temperature 20° C. Distilled water or artificial sea salts were added to filtered seawater to produce the desired salinities, and loose fitting plastic covers on the culture dishes reduced evaporation. Culture dishes with embryos were placed in thermostatically controlled constant temperature Hotpoint (#535)[3] incubators

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[2]R. B. Chapoton. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 69 p. Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

[3]Reference to trade names does not imply endorsement by the State University of New York at Stony Brook, or the National Marine Fisheries Service, NOAA.

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which maintained temperatures within ±0.5° C of 10°, 15°, 20°, and 25° C. Before the experiments began the embryos had been reared for 5 h at 20.5° C and 23.5‰, and had reached the early blastodisc stage of development. By the time of the next observations, about 5 h later, water temperature in the culture dishes had reached the desired incubation temperatures. Development data were mathematically adjusted for the delay in attaining experimental temperatures—see Results.

Developing embryos were observed with a stereomicroscope at intervals of about 4-6 h. Dead embryos were counted and removed, and stage of development of most live embryos was recorded. The basic nine-stage staging classification (Table 1) used in this research was similar to that used by Farris (1958, 1961). I refined this staging scheme by distinguishing among an early, middle, and two late periods within the nine stages. Early and late periods within a stage of development were quantified by subtracting 0.2 from, and adding 0.3, and 0.5, respectively, to the stage number.

TABLE 1.—Fish embryo stages of development used for *Brevoortia tyrannus*.

Stage	Description
1	Fertilized eggs prior to cell division to 8-cell stage
2	Eight-cell stage to completion of blastodisc formation
3	Blastodisc formation to germ ring halfway around egg
4	Germ ring halfway around egg to just prior to blastopore closure
5	Blastopore closure to tail bud beginning to separate from the yolk
6	Tail bud free of yolk to caudal one-eighth of body free of the yolk
7	Caudal one-eighth of body free of yolk to caudal one-fourth of body free of yolk
8	Caudal one-fourth of body free of yolk to fin fold moderately wide and tail portion of embryo rotated out of embryonic axis and tail approaching head
9	Tip of tail approaching head to hatching

RESULTS

Survival to hatching in the *B. tyrannus* rearing experiments was low, particularly at the 10° C incubation temperature. Temperature but not salinity had a significant effect on embryonic mortality in these experiments (Table 2). Testing by a posteriori sum of squares simultaneous test procedure (SS-STP) (Sokal and Rohlf 1969) revealed that embryonic mortality was significantly greater ($P<0.05$) at the 10° C incubation temperature, and not significantly different ($P>0.05$) at 15°, 20°, and 25° C.

During the experiments it became clear that most embryo deaths occurred during the first half of embryogenesis, and in particular, just prior to blastopore closure (prior to stage 5 in the staging classification used in this research) (Table 3).

TABLE 2.—Data on mortality (upper) and two-way ANOVA (lower) with replication to determine the effect of temperature and salinity on *Brevoortia tyrannus* embryos. Mortality data are the proportion of dead embryos (p). ANOVA performed on angular transformed (arc sine $p^{0.5}$) data.

	Temperature			
Salinity	10° C	15° C	20° C	25° C
10‰	0.96	0.64	0.68	0.56
	.92	.60	.92	.72
20‰	1.00	.72	.76	.64
	1.00	.56	.60	.80
30‰	1.00	.48	.56	.68
	1.00	.48	.52	.68

Source of variation	df	SS	MS	F_s
Subgroups	11	5,327.935	484.358	
Temperature	3	4,640.063	1,546.688	49.6**
Salinity	2	106.056	53.028	1.7 ns
Temp. × Salinity	6	581.816	96.969	3.1 ns
Within subgroups (error)	12	373.950	31.162	
Total	23	5,701.885		

** = $P<0.01$; ns = $P>0.05$.

TABLE 3.—Percent (cumulative) mortality of *Brevoortia tyrannus* embryos prior to and after blastopore closure (stage 5) reared at four temperatures in the laboratory.

Temperature (° C)	Mortality to stage 5 (%)	Mortality to stage 9 (%)
10	94	98
15	49	58
20	59	67
25	63	68

When the difference in frequency of embryo deaths prior to stage 5 and from stage 5 to stage 9 was tested at each of the four incubation temperatures, mortality was not significantly different throughout development at 10° C, but was significantly greater prior to stage 5 at the 15°, 20°, and 25° C incubation temperatures (Table 4).

Data on embryonic age and stage of development were virtually identical in replicate culture dishes and for embryos reared at the same temperature but different salinity. Therefore, analysis was restricted to temperature effects on development rate.

TABLE 4.—Significance of difference in deaths of *Brevoortia tyrannus* embryos prior to and after blastopore closure (stage 5) at four temperatures. Test is 2 × 2 test of independence using the G-statistic with Yates' correction.

Temperature	Development stage	Alive	Dead	Sum	% dead	G_{adj}
10° C	Prior to stage 5	9	141	150	94.0	
	Stage 5-stage 9	3	6	9	66.7	3.639 ns
15° C	Prior to stage 5	77	73	150	48.7	
	Stage 5-stage 9	63	14	77	18.2	19.922**
20° C	Prior to stage 5	62	88	150	58.7	
	Stage 5-stage 9	49	13	62	21.0	24.684**
25° C	Prior to stage 5	55	95	150	63.3	
	Stage 5-stage 9	48	7	55	12.7	42.685**

ns = $P>0.05$; ** = $P<0.01$.

Brevoortia tyrannus embryos used in the experiments were fertilized and reared at 20.5° C and 23.5‰ for the first 5 h of embryogenesis. To adjust development data for the delay in attaining experimental temperatures, correction factors were calculated to estimate the age embryos would have been at the beginning of the experiment had the embryos been incubated at experimental temperatures from fertilization. Since at 20°±0.5° C incubation temperature was constant throughout development, the correction factor used was the ratio of development time to stage 9 for embryos reared at 10°, 15°, and 25° C relative to development time to stage 9 at 20° C. Correction factors should be approximately proportional to development rates at different temperatures if the effect of delay in attaining experimental temperatures is small relative to incubation time to stage 9, and development rates are linear, as they appear to be (experimental (unadjusted) data points in Figure 1). When the experiments began, embryos had reached the early blastodisc stage of development; the age at that stage, therefore, for each incubation temperature, was estimated by multiplying the appropriate correction factor by 5 h. Development data were adjusted by adding to or subtracting from experimental data the difference between the expected age at the early blastodisc stage at 10°, 15°, and 25° C from the age observed at 20° C. Derivations of correction factors are presented in Table 5, and adjusted data on embryonic development in Table 6.

Age was regressed on embryonic stage of development (S) by least-squares linear regression.

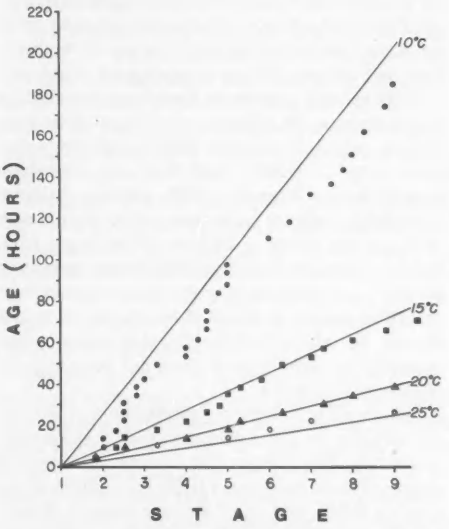

FIGURE 1.—Symbols represent age-stage relations of most *Brevoortia tyrannus* embryos in experiments (unadjusted data) at 10° C, 15° C, 20° C, and 25° C. Solid lines are regression lines of embryo age (A) on developmental stage (S) with experimental data adjusted for preexperimental time and temperature. Regression equation at 10° C is $A = 25.476(S - 1)$; 15° C, $A = 9.295(S - 1)$; 20° C, $A = 4.948(S - 1)$; 25° C, $A = 3.311(S - 1)$.

TABLE 6.—Adjusted data on the embryonic development of *Brevoortia tyrannus* incubated at four temperatures.

Temperature	Age (h)	Embryonic stage	Temperature	Age (h)	Embryonic stage
10° C	24.0	1.8	15° C	8.8	1.8
	28.5	2.0		13.0	2.3
	33.0	2.0		17.5	2.5
	36.5	2.3		21.5	3.3
	41.5	2.5		25.5	4.0
	45.5	2.5		30.0	4.5
	49.5	2.5		33.0	4.8
	53.5	2.8		38.5	5.0
	57.5	2.8		42.0	5.3
	61.5	3.0		46.0	5.8
	68.5	3.3		53.0	6.3
	72.5	4.0		57.0	7.0
	76.5	4.0		61.0	7.3
	80.5	4.3		65.0	8.0
	85.5	4.5		70.0	8.8
	89.5	4.5		74.0	9.3
	94.5	4.5	20° C	5.0	1.8
	103.0	4.8		10.0	2.5
	107.0	5.0		14.0	4.0
	113.0	5.0		18.5	5.0
	117.0	5.0		22.5	5.3
	129.5	6.0		27.0	6.3
	137.5	6.5		30.5	7.3
	151.0	7.0		35.0	8.0
	156.0	7.5		39.0	9.0
	163.0	7.8	25° C	3.5	1.8
	170.5	8.0		9.0	3.3
	181.5	8.3		13.0	5.0
	194.0	8.8		17.0	6.0
	205.0	9.0		21.0	7.0
				25.0	9.0

TABLE 5.— Derivation of correction factors to adjust development data for differences between experimental and preexperimental temperatures during the first 5 h of embryogenesis in *Brevoortia tyrannus*.

Item	10 ° C	15° C	20° C	25°
Hours to stage 9 in experiment (unadjusted data)	186	57	39	27
Ratio of hours to stage 9 relative to 39 h at stage 9 at 20° C	4.77	1.72	1.00	0.69
Expected age (h) at early blastodisc stage. Line 2 × 5 h	24.0	8.6	5.0	3.5
Correction factor to unadjusted data. Line 3 − 5 h	+19.0	+3.6	0	−1.5

$$\text{Age} = B\,(S - 1). \quad (1)$$

The results (Table 7; Figure 1) showed that age stage relations were nearly perfectly linear as a function of incubation temperature, and the regressions were highly significant (Table 7). Analysis of variance of the regression coefficients showed that development rates were highly significantly different among temperatures ($F(3, 57) = 1{,}405.0$; $P<0.001$). (Regression coefficients (B's) of Table 7 represent the "stage" development rate (units: hours/stage) of embryogensis in *B. tyrannus* and are only meaningful when used in context with the embryo staging classification in Table 1.)

The linear relationship between the logrithm of the stage development rate of *B. tyrannus* (B) and temperature (T in degrees Celsius) (Figure 2) is expressed by the following:

$$\log_{10} B = 1.923 - 0.059\,T. \quad (2)$$

The temperature coefficient (Q_{10}) for *B. tyrannus* embryonic development from fertilization to hatching at 10° to 25° C determined by Equation (2) is 3.89. The relation between the logarithm of the embryonic development rate of fish and temperature, though, is not necessarily linear (Kinne and Kinne 1962; Fonds et al. 1974), and, therefore, best predictions of stage development rates of *B. tyrannus* embryos (B) incubated at constant temperature (T in degrees Celsius) are obtained from the explicit empirical equation:

$$\log_{10} B = -0.193 + 17.193\,T^{-1} + 34.090\,T^{-2} - 461.276\,T^{-3}. \quad (3)$$

TABLE 7.—Linear regression of *Brevoortia tyrannus* embryo age (A) in hours since fertilization on morphological stage of development (S).

Temperature	Regression equation	F ratio	P	r^2
10° C	$A = 25.476\,(S - 1)$	$F(1, 29) = 7{,}110.8$	***	0.996
15° C	$A = 9.295\,(S - 1)$	$F(1, 15) = 6{,}427.6$	***	.998
20° C	$A = 4.948\,(S - 1)$	$F(1, 8) = 3{,}386.8$	***	.998
25° C	$A = 3.311\,(S - 1)$	$F(1, 5) = 1{,}258.6$	***	.996

*** = $P<0.001$.

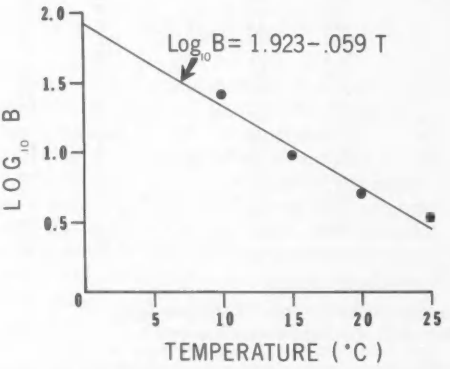

FIGURE 2.—Linear regression of the $\log_{10}$ of the "stage" development rate of *Brevoortia tyrannus* embryos (B) on temperature (T). Coefficient of determination = 0.96; SE regression coefficient = 0.0084.

DISCUSSION

The *B. tyrannus* embryo rearing experiments were mainly designed to determine effects of temperature and salinity on development rate; however, the results also have a bearing on temperature and salinity effects on embryonic survival.

Wide salinity tolerances have been reported for many marine fish embryos (Holliday 1969). *Brevoortia tyrannus* embryos have a salinity tolerance range >10-30‰, and they are, therefore, euryhaline by Kinne's (1964) criteria. Atlantic menhaden embryos have been collected in water with salinity as low as 18.15‰ (Wheatland 1956), but according to Reintjes (1967) most spawning occurs ". . . in the ocean or in inshore waters with salinities similar to those of the ocean." It would appear, therefore, that *B. tyrannus* embryos can tolerate low salinity conditions not normally encountered in nature.

Details of the salinity-development rate relation are species dependent, and they may be complicated by the influence of salinity on dissolved oxygen (Kinne and Kinne 1962; Forrester and Alderdice 1966), and the hatching process (Kinne and Kinne 1962; Alderdice and Velsen 1971); but, within limits, salinity effects on embryonic development rates tend to be small or insignificant for most marine fishes studied (e.g., McMynn and Hoar 1953; Alderdice and Forrester 1968, 1971a, b). Slight but apparently significant positive relations between embryonic development rate and salinity have been reported in some oceanic species (Forrester and Alderdice 1966; Laurence and Rogers 1976). Embryos of oceanic species are probably more sensitive to low salinity and changes in salinity than estuarine species. In the experiments presented in this paper, salinity between 10 and 30‰ had no noticeable effect on the embryonic development rate of *B. tyrannus*.

Brevoortia tyrannus embryo mortality was high at the 10° C incubation temperature. In a preliminary laboratory experiment, naturally fertilized *B. tyrannus* embryos at the blastodisc stage of development (stage 2) from field plankton collections (14.7° C, 24‰) failed to develop beyond stage 4 when the incubation temperature was lowered to 6°±1° C. The lowest temperatures at which Atlantic menhaden embryos have been collected in the field generally range between 10° and 13° C (Perlmutter 1939; Wheatland 1956; Richards 1959; Herman 1963), but they have been reported in water as low as 7.7° C (Mundy[4]). The available information, therefore, indicates that while spawning rarely occurs in water <10° C, the low lethal temperature of *B. tyrannus* embryos is probably about 7° C.

The temperature range in the experiments (10°-25° C) was not sufficiently wide to determine the upper temperature tolerance of *B. tyrannus* embryos, which survived equally well at 15°, 20°, and 25° C. There are no references in the literature of Atlantic menhaden embryos in nature in water >25° C.

A number of investigators have noted that high fish embryo mortalities tend to occur during gastrulation and just prior to or during hatching (McMynn and Hoar 1953; Alderdice and Forrester 1971a; Laurence and Rogers 1976; and others). High mortalities of *B. tyrannus* embryos occurred only during gastrulation.

Generally there is a linear or slightly curvilinear relationship between the logarithm of the development rate of fish embryos and temperature (see Blaxter 1969, fig. 4; Williams 1975; and others). The embryonic development rate of *B. tyrannus* followed this general rule (Figure 2).

Brevoortia tyrannus embryo age-stage relations at each of the four incubation temperatures were nearly perfectly linear (Figure 1; Table 7). These results imply a) the durations of the stages (Table 1) are approximately equal, b) the effect of the four incubation temperatures on rate of development of *B. tyrannus* embryos was relatively the same in all stages, and c) the stages of development can be used to estimate the age of embryos if the incubation temperature is known and constant.

A simple method of predicting the age of a *B. tyrannus* embryo at any stage of development from Table 1, incubated at any constant temperature (degrees Celsius) is to solve Equations (3) and (1), in succession for B and age. At low temperatures precision of the age estimate decreases because duration of stages increases. At temperatures in which menhaden commonly spawn (15°-20° C), this method yields an estimate of embryo age with an average expected error from stage duration of between 1.3 and 2.3 h (average error = ¼ × stage development rate).

Kuntz and Radcliffe (1917) and Hettler (1970) gave the incubation time of *B. tyrannus* embryos, but Kuntz and Radcliffe did not specify the incubation temperature. Hettler (1970) observed hatching within 66-74 h at an average incubation temperature of about 15.5° C (range 11.5°-19.5° C). The embryo age calculated for stage 9 at 15.5° C from the age prediction equations is 68.8 h, which compares well with Hettler's observation.

Other methods have been developed which estimate age of fish embryos. Simpson (1959) and Brown and Hassler (1973) constructed nomographs recording the influence of temperature on durations of embryonic stages of *Pleuronectes platessa* and *Morone saxatilis*, respectively. Ahlstrom (1943) and Talbot (1977) used regression analysis to describe the relationship between temperature and durations of fish egg stages, but their methods require calculating separate regressions for each development stage and temperature and does not allow interpolation of development rates between temperatures. Zweifel and Lasker (1976) applied the Laird-Gompertz growth equation to incubation times and embryonic growth (extrapolated from early posthatch growth) of fish embryos. The Laird-Gompertz equation appears to give good predictions of fish embryo growth, but its computation requires solving a multiparameter equation by iteration for each incubation temperature. The fish embryo age estimation method described in this paper is simple and has broader practical applications than the methods above. Together Equations (3) and (1) accurately describe the age-stage-temperature relations of *B. tyrannus* embryos at easily identifiable stages, during the entire embryonic development, and over a wide range of temperatures. Embryo age prediction equations can be calculated for other species in the manner described

[4]Mundy, B. C. 1974. Order Clupeiformes Family Clupeidae *Brevoortia tyrannus* (Latrobe), Atlantic menhaden. *In* H. M. Austin (editor), Preoperational ecological monitoring program of the marine environs at the Long Island Lighting Company (LILCO) nuclear power generating facility, Shoreham, Long Island, N.Y., vol. 2, sect. 5, p. 15-20. Contract SR-72-32. LILCO Community Relations, 250 Old Country Road, Mineola, NY 11501.

here for *B. tyrannus*, and, if necessary, the precision of embryo age estimates by this method can be improved by increasing the number of development stages of approximately equal duration in the embryo stage classification scheme.

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DISTRIBUTION AND MOVEMENTS OF RISSO'S DOLPHIN, *GRAMPUS GRISEUS*, IN THE EASTERN NORTH PACIFIC

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ABSTRACT

Records of occurrence are summarized from 22 strandings/collections and 210 sighting records from miscellaneous sources. When available, levels of effort have been identified and utilized to interpret the trends in distribution and movement apparent from the data. Risso's dolphins occur from at least the Equator (southern end of area examined) north to approximately latitude 50° N, with regions of apparently very low density centering at about latitude 20° and 43° N. Records from northern and inshore portions of the range were most numerous during late spring through early fall. Both within and among years, periods of greatest abundance for the species north of latitude 43° N, near Monterey Bay, California, and over the southern California continental borderland appear to correspond with protracted periods of warm water. Groups contained from 1 to an estimated 220 animals, about a geometric mean of 10.7. An estimated 76.4% of the groups contained fewer than 20 animals.

The Risso's dolphin or gray grampus, *Grampus griseus*, is widely distributed in tropical and temperate waters around the world. It occurs on the western side of the Atlantic Ocean from at least Newfoundland (approximately lat. 50° N, Leatherwood et al. 1976) south to Cape Horn (approximately lat. 53° S, Norris[6]), and in the Gulf of Mexico (True 1885; Gunter 1954; Paul 1968) and the Caribbean (Caldwell et al. 1971). On the eastern side of the Atlantic it occurs from the Shetland Islands, Scotland (Turner 1892), south to the Cape of Good Hope (approximately lat. 34° S, Barnhard 1954), including the North Sea (Schultz 1970), and throughout the Mediterranean Sea complex (Bazzauti 1910; Tamino 1953; Pilleri and Gihr 1969), including the Adriatic (Trois 1883; Ninni 1901; Carrucio 1906; Riedl 1965; Pilleri and Gihr 1969). It also occurs in the Red Sea (Hershkovitz 1966) and in the Indian Ocean (Ellerman et al. 1953; Weber 1923), at least to the Indo-Australian Archipelago, and on the west side of the Pacific Ocean from the Commander Islands (approximately lat. 55° N, Sleptsov 1961) south to New Zealand (Hector 1873; Parker 1934; Alpers 1960; Gaskin 1968; Baker 1974), including the South China Sea, the Philippine Sea (Baker 1974), and the waters around the New Hebrides (Maxwell 1952), the Solomon Islands (Dawbin 1966), and New Guinea (Gaskin 1972). On the eastern side of the Pacific it has been reported from the Bering Sea (Clark 1945) and British Columbia (Guiguet and Pike 1965) south to Valparaiso, Chile (Aguayo 1975), and Cape Horn (Norris see footnote 6), including the Gulf of California (Leatherwood et al. 1979). That Risso's dolphins are present in Hawaiian waters as well is indicated by three sightings and a stranding on Maui in 1977 (E. W. Shallenberger[7]). Davies (1963) remarked on the species' overall distribution that it is basically tropical but extends its ranges poleward to overlap the ranges of temperate forms, though they generally do not penetrate so far into high latitudes. In all areas, the species' distribution is known only from infrequent stranding records and at-sea sightings, and published accounts continue to restate those records, often without adding substantial new data. Details of the animal's distribution and movements are not reported. This paper reviews the information available through 1975 on Risso's

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[6]Norris, K. S. 1968. Cruise report of the R/V *Hero*, November 12-December 11, Valparaiso-Puntarenas, Chile, 11 p. Coastal Marine Laboratory, University of California, Santa Cruz, CA 95060.

[7]E. W. Shallenberger, Curator, Sea Life Park, Waimanalo, HI 96795, pers. commun. to Leatherwood September 1977.

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dolphins in the portion of the eastern Pacific from the Equator and long. 145° W north and east respectively, from strandings, collections, and sighting records, and examines the data for patterns in distribution, movement, and seasonal occurrence.

METHODS

Inherent in the approach to this paper is the opinion that for this as for other areas, there are numerous scientists and organizations which have small amounts of information of little significance alone, but when the data are combined, they can yield a better understanding of what is known about a given cetacean species (e.g., see Leatherwood and Walker (1979) on *Lissodelphis borealis*).

We reviewed previously published records of at-sea sightings of Risso's dolphins in the study area (Table 1). We then examined over 250 previously unpublished reports of sightings of the species in the area from 1958 to 1975[6] for reliability of identification. Interviews with observers and photos assured us of the accuracy of most records. Descriptions of animals with slate gray to nearly all-white coloration, extensive scarring, a bifurcated melon, and a prominent dark dorsal fin, all distinctive characteristics of Risso's dolphins (Figure 1), aided in verification of the remainder. We discarded questionable records.

Many of the reports included estimates of herd size. Since many of these were stated as ranges (e.g., 30-40 animals), we used the midpoint of each estimate. If the estimate was such that the midpoint was a half number (e.g., an estimate of 10-15 animals) we took the lower of the numbers (e.g., 12).

Some records also included measurements of sea surface temperature at or near the location of the observation. The few of those most important to interpreting apparent trends in the more northern portions of the study area were used, along with annual summaries of temperature trends.

Incidental sighting records alone cannot be used to reliably determine trends in distribution, movements, or abundance. Data on sighting effort are essential. Although a few major marine surveys have been conducted in the study area, effort is difficult to quantify for most other sources of

[6]A summary of verified records of observations of *Grampus griseus* in the northeast Pacific is available from Leatherwood or Perrin.

TABLE 1.—Previously published at-sea sightings of Risso's dolphins in the eastern North Pacific. In the few cases where collections were reported, as in Orr (1966), herds from which animals were collected are not included as sight records.

Source	Date	Location	Number in school
Hubbs (1960)	? 1960	Isla Guadalupe, Mexico	Unreported
Fiscus and Niggol (1965)	18 Mar. 1958	38°30' N, 124°15' W	"Many animals"
Guiguet and Pike (1965)	22 July 1958	50°00' N, 145°00' W	1
Fiscus and Niggol (1965)	27 Jan. 1959	36°45' N, 122°33' W	3
Fiscus and Niggol (1965)	4 Feb. 1959	35°12' N, 122°05' W	50+
Fiscus and Niggol (1965)	8 Feb. 1959	35°44' N, 122°43' W	2
Fiscus and Niggol (1965)	18 Mar. 1959	41°42' N, 125°53' W	10+
Fiscus and Niggol (1965)	28 Mar. 1959	40°52' N, 125°19' W	5
Guiguet and Pike (1965)	11 Oct. 1959	50°00' N, 145°00' W	6
Guiguet and Pike (1965)	15 Aug. 1960	50°00' N, 145°00' W	5
Guiguet and Pike (1965)	4 Sept. 1960	50°00' N, 145°00' W	4
Daugherty (1972)	? 1971	Midway between San Diego (Pt. Loma) and San Clemente Island, Calif.	50
Leatherwood et al. (1972)	? 1971	05°00' N, 87°04' W	Unreported
Leatherwood et al. (1972)	? 1971	11°00' N, 109°30' W	Unreported
Leatherwood et al. (1979)	13 Feb. 1974	24°52' N, 108°58' W	5-10
Leatherwood et al. (1979)	13 Feb. 1974	28°21' N, 112°30' W	2

FIGURE 1.—Risso's dolphins off southern California, 1973. The animal's distinctive whitish head (in adults), scarring, and high subtriangular dorsal fin enhance the reliability of "incidental" observational records. (Photo by G. E. Lingle, courtesy Naval Oceans Systems Center, San Diego, Calif.).

data. The following information on effort, from which we feel reliable trends may be determined, exists for the survey programs in the study area.

From San Diego to Equator—National Marine Fisheries Service (NMFS) observers, aboard tunaboats working primarily out of San Diego, Calif, surveyed the area from San Diego south to the Equator from 1966 through 1975. The majority of effort was concentrated in January and February, declining rapidly through April to no effort in the Commission Yellowfin Regulatory Area (CYRA) of the Inter-American Tropical Tuna Commission by the third quarter (Figure 2). It is evident that there has been very little effort in the nearshore portion of the tropical CYRA during the third and fourth quarters, although there were six chartered cruises between September and December. Far-offshore fishing and research activity continued throughout the year. Because the vessels return north to San Diego, running anywhere from 12 mi offshore to beyond the continental shelf off Baja California, effort appears to have been adequate throughout that area to detect major seasonal changes in composition of marine mammal fauna. This is the only program for the area for which extensive and quantified data on effort and sightings were available.

Since 1968, cruises of the Naval Ocean Systems Center, San Diego (NOSC, formerly Naval Undersea Center), have examined the continental shelf area off northwestern Baja California during winter and spring (October-December and February-April). Vessels of the Scripps Institution of Oceanography with marine mammal observers aboard have cruised extensively among the San Diego-Guadalupe Island-Cedros Island triangle for over 30 yr.

Southern California Continental Borderland—Survey effort has been extremely heavy over the continental shelf from Ensenada north to Point Conception. Norris and Prescott (1961) reported on activities of Marineland of the Pacific, primarily between Catalina and Santa Barbara Islands and the mainland shore near Los Angeles. Leatherwood (1974), Evans (1975), and Leatherwood and Walker (1979) summarized NOSC aerial

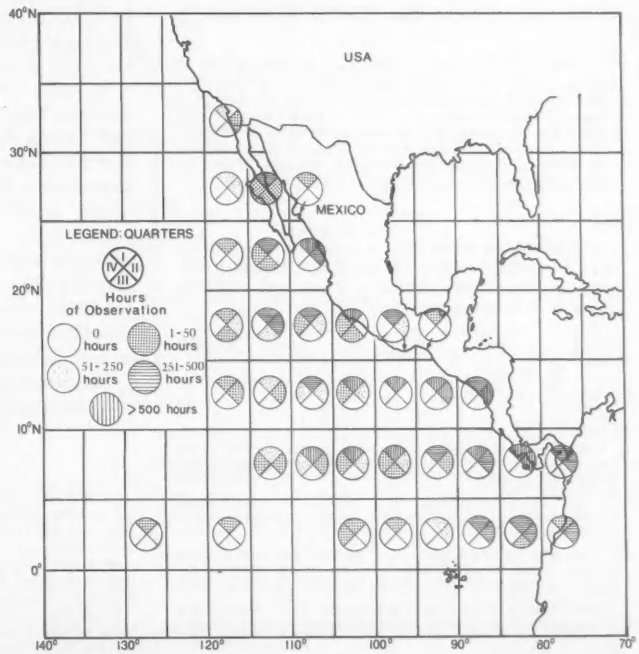

FIGURE 2.—Relative numbers of hours of observation by NMFS/SWFC observers aboard tunaboats in the eastern tropical Pacific by quarter of year, 1974-75.

and ship survey effort in this area for 1968-75. Norris et al.[9] summarized Bureau of Land Management (BLM) aerial and ship surveys during 1975 and 1976. Although variable by month, we consider this combined effort adequate at all seasons to have detected trends in composition of marine mammal fauna for the borderland and adjacent continental slope. Coverage was particularly thorough for the area in 1975, when NOSC and BLM programs overlapped.

Offshore Southern and Central California—During 1967 and 1968, cruises of the Smithsonian Institution's Pacific Ocean Biological Survey program surveyed the outer California Channel Islands and the area from lat. 29° to 37° N and seaward to long. 126° W during all quarters of the year. Marine mammal observations by experienced personnel were logged for all cruises (R. L. Brownell, Jr.[10]).

Offshore Baja California North to Washington—More recent coverage of the area from lat. 25° N to Washington State, primarily offshore, has been provided by NMFS observers out of the Southwest Fisheries Center (SWFC) placed on commercial albacore boats. In 1971-75, observers aboard 15 working albacore boats reported marine mammal observations made between May and September from lat. 25° to 46° N (Table 2). Although the time and location of their activities varied annually with the albacore migration, coverage was generally restricted to summer and generally moved north as the season progressed.

Nearshore Central California—Recent aircraft and ship surveys by the University of California at Santa Cruz have examined the area from about Point Conception north, with the most extensive sampling effort in Monterey Bay. Coverage near Monterey Bay has been year-round (J. D. Hall[11]). Infrequent cruises by personnel from Hopkins Marine Station and Moss Landing Marine Laboratory have examined the same area (A. Baldridge[12]).

Oregon and North—With one important exception, recorded survey effort begins to decline as one moves north from California. NMFS albacore-boat observer programs conducted in the summer have extended north of Point Conception (Table 2), and one NOSC marine mammal cruise was conducted from San Diego to Kodiak, Alaska, in April 1971. The primary effort, however, including extensive coverage of the area from Seattle north through the Gulf of Alaska and northwest to the Aleutian Islands and the Bering Sea, has been that by cruises of the NMFS Northwest and Alaska Fisheries Center (NWAFC) Pelagic Fur Seal Research Program. Over the past 10 yr, these cruises have primarily spanned the fall and winter months (C. H. Fiscus[13]). Other research cruises by NWAFC have begun in the Seattle area and worked south to southern California in January, February, and March (Fiscus and Niggol 1965), while still others beginning in San Francisco have worked south to the Revillagigedo Islands in winter and spring (Rice 1963a, b).

The remainder of the sighting effort for the northeastern Pacific is difficult to assess, though it

[9]Norris, K. S., T. P. Dohl, R. C. Guero, L. J. Hobbs, and M. W. Honnig. 1976. Cetaceans; numbers, distribution, and movements in the southern California Bight. 192 p. Draft report to Bureau of Land Management, OCSEAP, from Coastal Marine Laboratory, University of California, Santa Cruz, CA 95060.

[10]R. L. Brownell, Jr., U.S. National Museum of Natural History, National Fisheries and Wildlife Laboratory, Wash., DC 20560, pers. commun. to Leatherwood June 1975.

TABLE 2.—Months during 1961-75 in which marine mammal watches were maintained aboard one or more albacore vessels (×) in the eastern Pacific (1971-75), by 5° increments of latitude. A total of 15 vessels were involved.[1-4]

Lat. (° N)	May	June	July	August	September
45-50				×	×
40-45		×	×	×	×
35-40		×	×	×	
30-35	×	×	×		
25-30	×	×	×		

[1]Laurs, R. M., and Associates. 1972. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1971 and 1972. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif., 78 p.

[2]Laurs, R. M., and Associates. 1973. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1973. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif.

[3]Laurs, R. M., and Associates. 1974. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1974. Admin. Rep. 25-74-47, SWFC, NMFS, NOAA, La Jolla, Calif.

[4]Laurs, R. M., R. J. Lynn, and R. N. Nishimoto. 1975. Report of joint National Marine Fisheries Service - American Fisherman's Research Foundation albacore studies conducted during 1975. Spec. Publ. SWFC, NMFS, NOAA, La Jolla, Calif.

[11]J. D. Hall, U.S. Fish and Wildlife Service, Office of Biological Services, 800 A Street, Suite 110, Anchorage, AK 99501, pers. commun. to Leatherwood August 1975.

[12]A. Baldridge, Library, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Fla.; present address: Hopkins Marine Station, Pacific Grove, CA 93950, pers. commun. to Leatherwood 1975.

[13]C. H. Fiscus, Northwest and Alaska Fisheries Center Marine Mammal Division, NMFS, NOAA, 7600 Sand Point Way NE Seattle, WA 98115, pers. commun. to Leatherwood June 1976.

is clearly sporadic and has concentrated on coastal regions near population centers.

The areas of coverage of the most important programs considered in this report are summarized in Figure 3. (The expanded area coverage of the SWFC tunaboat-observer program is shown in Figure 2).

RESULTS

Strandings and Collections

As nearly as we can determine, 22 strandings and/or collections of specimens of *G. griseus* have been recorded in the northeastern Pacific since about 1872 (Figure 4).

1. (Published). In the late 19th century, probably in 1872, although the exact date is undeterminable, Charles M. Scammon obtained two lower jaws from Monterey, Calif. (Scammon 1874). Dall (1874) used these two lower jaws as the basis for his description of *G. sternsii,* later rejected as a species by True (1889) because it was indistinguishable from *G. griseus* (G. Cuvier 1812). One lower jaw and two teeth were deposited in the U.S. National Museum (USNM 13021), though True could not make his measurements agree with Dall's and tentatively said that it was "apparently neither the No. 1 nor the No. 2 of Mr. Dall's description" (True 1889). The whereabouts of the second mandible or, if True's

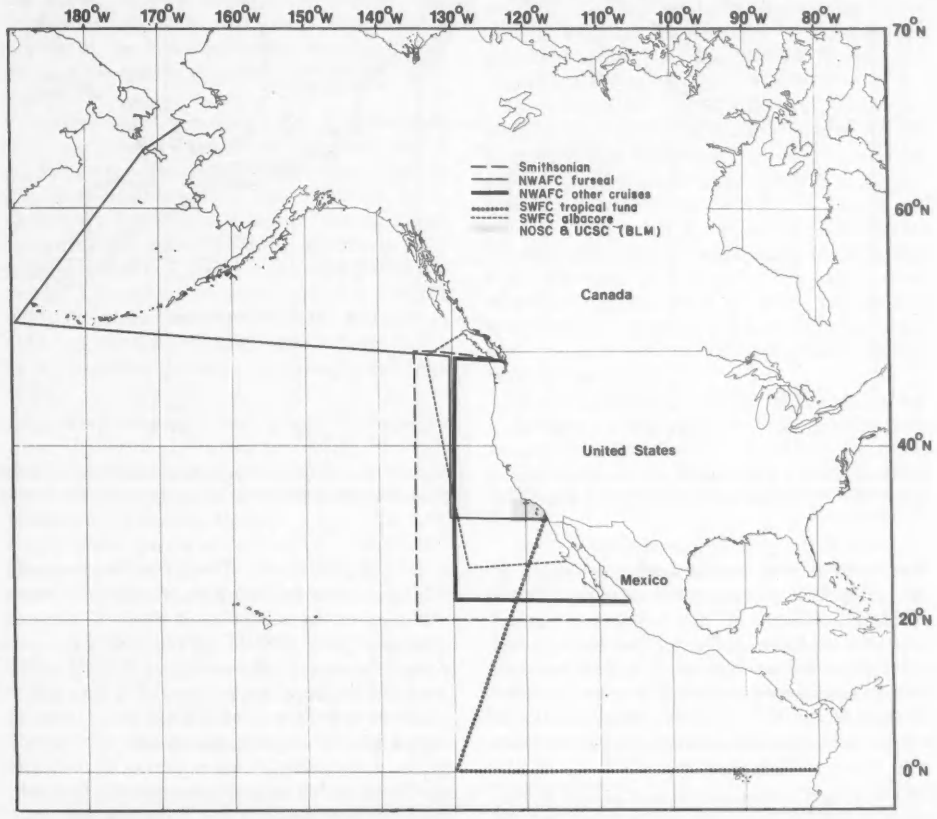

FIGURE 3.—The eastern North Pacific north of lat. 15° N, showing areas surveyed by major marine mammal survey programs (1958-75). See text for details of documentation.

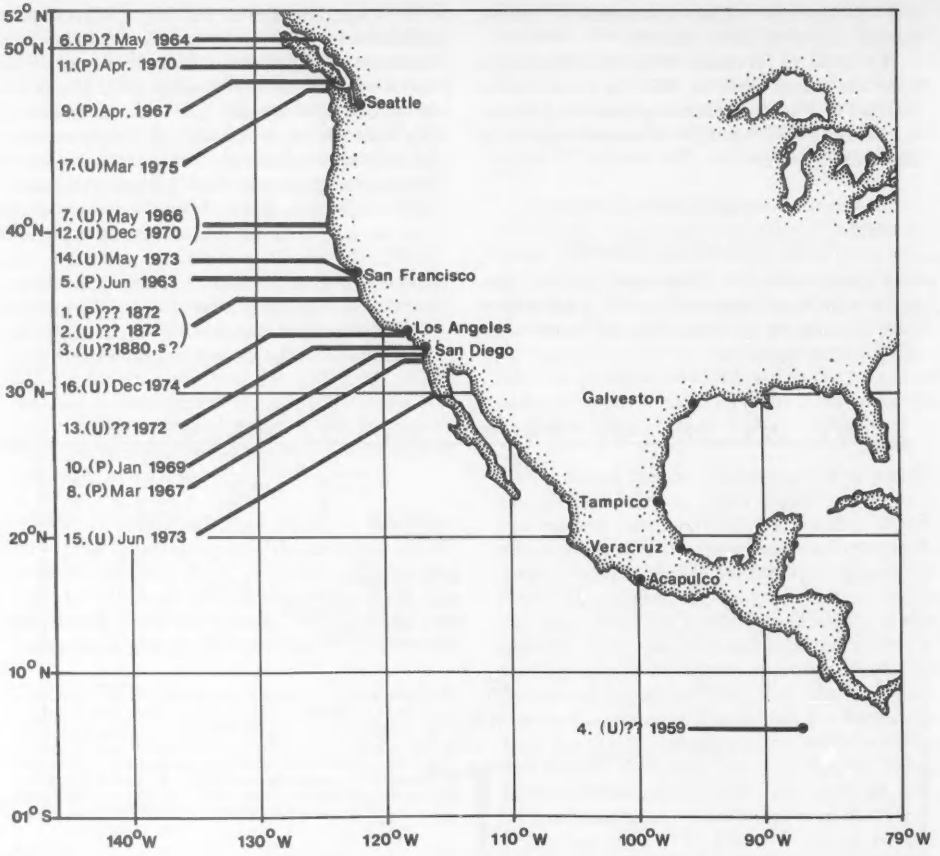

FIGURE 4.—Dates and approximate locations of strandings and collections of Risso's dolphins in the eastern North Pacific (1972-75) numbered in chronological order. The letters in parentheses indicate whether the record has (P) or has not (U) been previously published.

observations are correct, both mandibles described by Dall, are unknown, as is the identity of USNM 13021.

2. (Unpublished). During the same period, exact date also undeterminable, Scammon collected a second specimen which he also forwarded to True at the U.S. National Museum (USNM 21163). Like the first, this specimen was reportably taken in Monterey Bay, Calif. (C. H. Gilbert[14]).

3. (Unpublished). There are three remaining specimens from the Pacific coast of North America in the collection of the U.S. National Museum. One (USNM 28066) was purchased from fishermen in Monterey; one (USNM 49895) was taken from an unidentified locality in California; and the third (USNM 49347) was collected by C. H. Gilbert, presumably also in Monterey. Interestingly, in referring to this last specimen in his correspondance with Dall, Gilbert (see footnote 14) wrote "In addition to that, I have the complete skeleton of a calf about 6 months old. The species is abundant in Monterey

[14]C. H. Gilbert undated letter to W. Dall, in possession of Hubbs.

Bay and additional specimens could be secured for you if you desire."

4. (Unpublished). In 1959, a single lower jaw identifiable as that of a Risso's dolphin was brought to Hubbs from Isla de Coco ("Cocos Island"), lat. 05°32′ N, long. 87°04′ W. The location of the specimen is currently unknown.

5. (Published). On 11 June 1963, a 325.0 cm male apparently dead from gunshot wounds stranded on the beach 0.9 km from Princeton by the Sea, San Mateo, Calif. The account of the stranding and its workup includes a description of the specimen, analysis of stomach contents, miscellaneous external measurements and organ weights, and some cranial measurements (Orr 1966). The specimen was deposited in the collection of the California Academy of Sciences, San Francisco (CAS 13461, Orr 1966). This account represents the first continental eastern Pacific record of the species published since the late 19th century.

6. (Published). In May 1964, a single 11-ft (334.0 cm) Risso's dolphin was observed alive in Big Bay on the west side of Stuart Island, British Columbia (approximately lat. 50°20′ N, long. 125°00′ W). The animal was shot, dissected, and discarded. The caudal peduncle and flukes were later recovered and placed in the collection of the British Columbia Provincial Museum (BCPM 9077). The animal was reported by the collectors to have been feeding on squid and to have had a heavy intestinal parasite load (Guiget and Pike 1965).

7. (Unpublished). On 13 May 1966, Robert E. Jones (Museum of Vertebrate Zoology, Berkley, Calif.) found a long dead but complete carcass of a stranded male approximately 10 km south of Cape Mendocino, Humbolt County, Calif. The total length of the specimen was 9 ft 7.5 in (293.9 cm). The skull and left flipper were collected and deposited at the Humboldt State University (HSC-66-4).

8. (Published). On 18 March 1967, an adult male stranded alive at Cantomar (Rosarita Beach), 42 km south of Tijuana, Baja California, Mexico (approximately lat. 32°18′ N, long. 117°00′ W). It was taken to Sea World in San Diego, Calif., where it survived for a short time. A photo of this animal appeared in the *San Diego Union* 28 March 1967 on page B-5. This specimen was 307.0 cm long (Harrison et al. 1969) and weighed 850 lb (386 kg) (measured by Hubbs). Although the specimen was reportedly deposited in the San Diego Natural History Museum, the Museum has no record of the specimen and its whereabouts are unknown.

9. (Published). On 20 April 1967, a 258 cm male apparently dead from a gunshot wound in the head was found stranded at Makkaw Bay, Wash. (lat. 48°19′ N, long. 124°40′ W). The dolphin had been dead an estimated 1 mo. Its stomach contained squid beaks and fragments. The skull and postcranial skeleton were preserved in the collection of NWAFC, NMFS, NOAA, Seattle, Wash. (Stroud 1968).

10. (Unpublished). On 21 January 1969, a 309 cm adult male stranded alive at Imperial Beach, San Diego County, Calif. The animal was taken to Sea World, San Diego, where it died the night of 21-22 January 1969. The complete skeleton was collected by Raymond M. Gilmore and deposited in the San Diego Natural History Museum (SDNHM 21554) (R. M. Gilmore[15]).

11. (Published). On 17 April 1970, a 266 cm male washed ashore on the east side of Vargas Island, British Columbia (lat. 49°10′ N, long. 125°58′ W). The skull, axial skeleton, and bones from one pectoral appendage were collected and placed along with a complete photo series (Photofile No. 51) in the collection of the Vertebrate Museum, Department of Zoology, University of British Columbia (UBC 9464). The report of the stranding includes external measurements, organ weights, and an analysis of stomach contents (Hatler 1971).

12. (Unpublished). On 26 December 1970, a male neonate was collected from the beach in Shelter Cove, Humboldt County, Calif. The entire specimen (Field No. WJH 71-1) was deposited at the Humboldt State University (HSU 1620) (W. J. Houck[16]).

13. (Unpublished). In August of 1970, responding to a radio call from local fishermen, F. Brocata and B. Falcone of Marineland of the Pacific investigated a call about an "albino" pilot whale which had been harpooned by fishermen between Santa Cruz and Santa Rosa Islands, Calif. When Marineland's research boat, the MV *Geronimo,* approached the whale, which turned out to be a Risso's dolphin, the animal managed to

[15]R. M. Gilmore, Research Associate, San Diego Natural History Museum, San Diego, CA 92112, pers commun. to Leatherwood 1975.

[16]W. J. Houck, Humboldt State University, Arcata, CA 95521, pers. commun. to Leatherwood 1975.

pull out the harpoon and swim away (W. A. Walker[17]).

14. (Unpublished). On 20 May 1973, an immature female was found stranded on southeast Farallon Island, off San Francisco, Calif. (approximately lat. 37°42′ N, long. 123°00′ W). The available measurements for the specimen are as follows: total length 270 cm, dorsal fin 27.5 cm, axilla-tip of flipper 5 cm, origin of flipper to tip of lower jaw 46.5 cm, anus-tip of lower jaw 178 cm, width of flukes 62 cm. The specimen was not collected (R. L. Brownell, Jr. see footnote 10).

15. (Published). On 18-19 June 1973, four females and a fifth animal of undetermined sex, all about 13 ft long (400 cm) and weighing 500-600 lb (73-77 kg) stranded alive at Punta Buffeo, Baja California, about 100 mi (160 km) south of San Felipe on the northwest coast of the Gulf of California (approximately lat. 29°55′20″ N, long 114° 26′20″ W). All five animals were towed out to sea (dead), and no materials were retrieved (Leatherwood et al. 1979).

16. (Unpublished). On 8 December 1974, a female stranded alive at the Manhattan Beach Pier, Los Angeles, Calif. (approximately lat. 33°55′ N, long. 118°25′ W). The animal was alive when it was collected by Marineland of the Pacific but died almost immediately after collection. It was photographed, measured, and necropsied at the Los Angeles County Museum of Natural History, where it is currently held as specimen LACM 47145. Detailed findings will be reported elsewhere (W. F. Samaras and D. R. Patten[18]).

17. (Unpublished). On 10 March 1975, a 348 cm female stranded alive at Port Discovery, Wash., in the Strait of Juan de Fuca (about lat. 48°02′ N, long. 122°52′ W), perhaps driven ashore by killer whales. The animal was recovered alive and taken to Seattle Marine Aquarium where it died on 11 March. The complete skeleton is in the collection of the NWAFC (No. 1975-1).

At-Sea Sightings

We found 16 previously published records of at-sea sightings of Risso's dolphins for the study area (Table 1) and 194 additional previously unpublished reliable records (see footnote 8) (Figure 5). When examined by latitude (Figure 5), the distribution of sightings falls into three major groups—those from the Equator to approximately lat 20° N (Zone I); those thence north to approximately lat. 43° N (Zone II); and those north of lat. 43° N (Zone III). Zones I and II are separated by a broad region characterized by very few sightings, centering at about lat. 20° N and extending from lat. 14° to 29° N. All except two sightings in that area of low density were within 60 mi of the Mexican coast, though seaward of the continental shelf. The separation between Zones II and III is less pronounced, centering at lat. 43° N and extending from lat. 38° to 45° N.

Regarding seasonality, records in Zone I are almost exclusively limited to first and second quarters, and the majority of those from Zone III are from the period July through October. Both of these apparent seasonal fluctuations result from the biases in observation effort discussed above. Those from Zone II are distributed throughout the year. Records from north of Point Conception (lat. 35° N) are most numerous in the third quarter (Figure 6).

Off southern California (approximately lat. 31°-35° N), records from 1959 to 1975 were sporadic, reaching a peak of 11 in 1974 (Table 3). Until 1971 the majority of sightings for the area were seaward of the 100-fathom curve; however, beginning in 1971 and increasing in frequency through 1974 (9 of 11) and 1975 (3 of 3), most sightings were over the continental shelf.

Although surface water temperatures were not reported for most sightings, Risso's dolphins have been sighted in waters ranging from 28° to 10° C. Sightings in Zone I cover the full range of temperatures reported for the area. Sightings off southern California in 1974 and 1975 were associated with water temperatures above 19° C. Of the 22

TABLE 3.—Summary of sightings of Risso's dolphins off southern California (about lat. 31°-36° N), 1959-75, showing the frequency of encounter over and seaward of the continental shelf.

Year	Total no. sightings	Over continental shelf	Seaward of continental shelf
1959	1	1	0
1960	1	1	0
1965	1	0	1
1966	3	0	3
1967	9	0	9
1968	3	1	2
1971	4	4	0
1972	4	4	0
1973	3	2	1
1974	11	10	1
1975	3	3	0

[17]W. A. Walker, 21 Barkentine Road, Rancho Palos Verdes, CA 93704, pers. commun. to Leatherwood 1975.

[18]W. F. Samaras, Research Associate, and D. R. Patten, Curator, Department of Mammals, Los Angeles County Museum of Natural History, Los Angeles, CA 90007, pers. commun. to Leatherwood 1975.

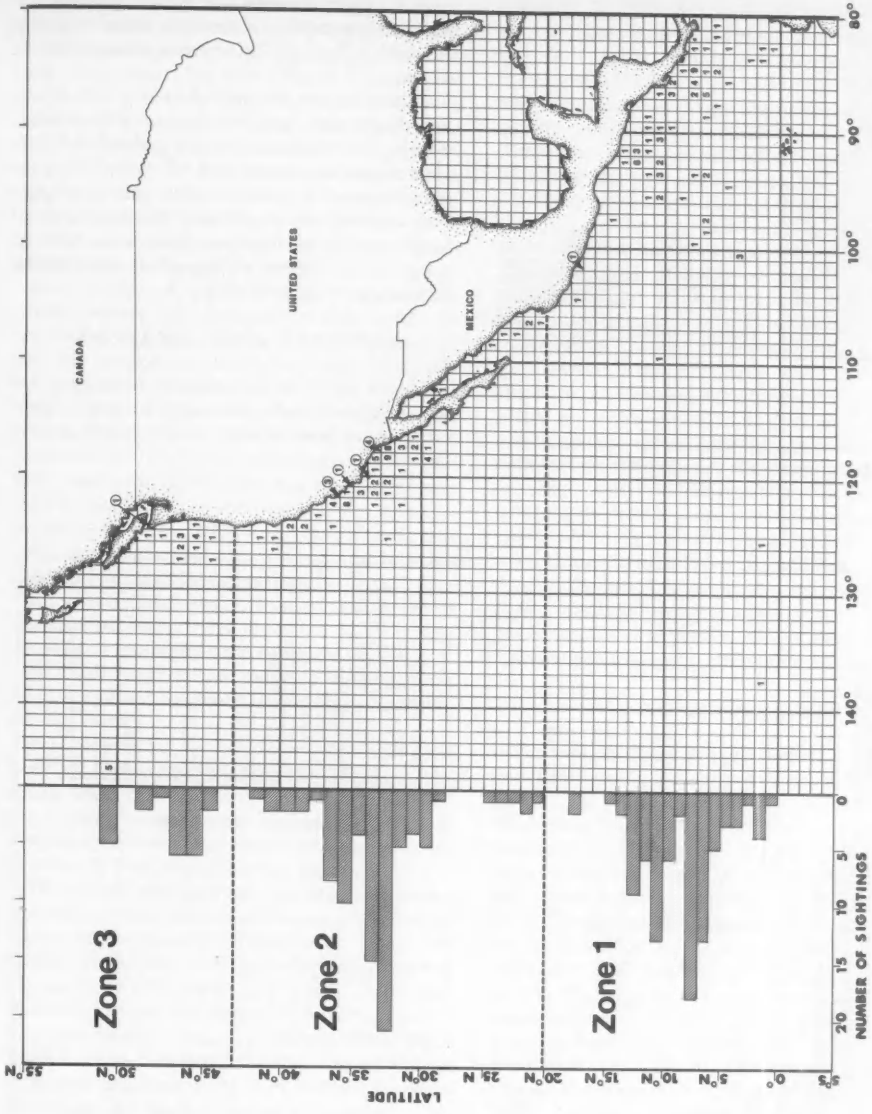

FIGURE 5.—At-sea sightings of Risso's dolphins in the eastern North Pacific (1958-75) by 1° square and frequency by 1° of latitude based on 210 sightings.

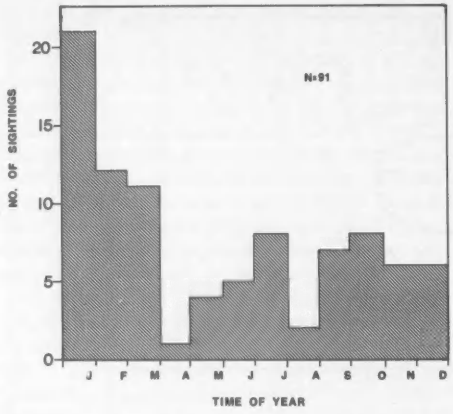

FIGURE 6.—Frequency of sightings of Risso's dolphins by month in Zone II in the eastern North Pacific (defined in Figure 5).

most northern records, the 4 from February to April were associated with water temperatures of 12° and 13° C, unusually high temperatures for the season.

Of the records, 12 published and 191 unpublished provided usable estimates of herd sizes. Numbers of animals sighted ranged from 1 to 220, about a geometric mean of 10.65. About 75% of the groups contained fewer than 20 animals (Figure 7). No statistically significant differences could be demonstrated among herd sizes from different zones (I, II, III) or different seasons (Mann-Whitney U Test, $\alpha = 0.05$).

SUMMARY AND DISCUSSION

Risso's dolphins are clearly abundant and widely distributed year-round in tropical and warm temperate waters of the northeastern Pacific.

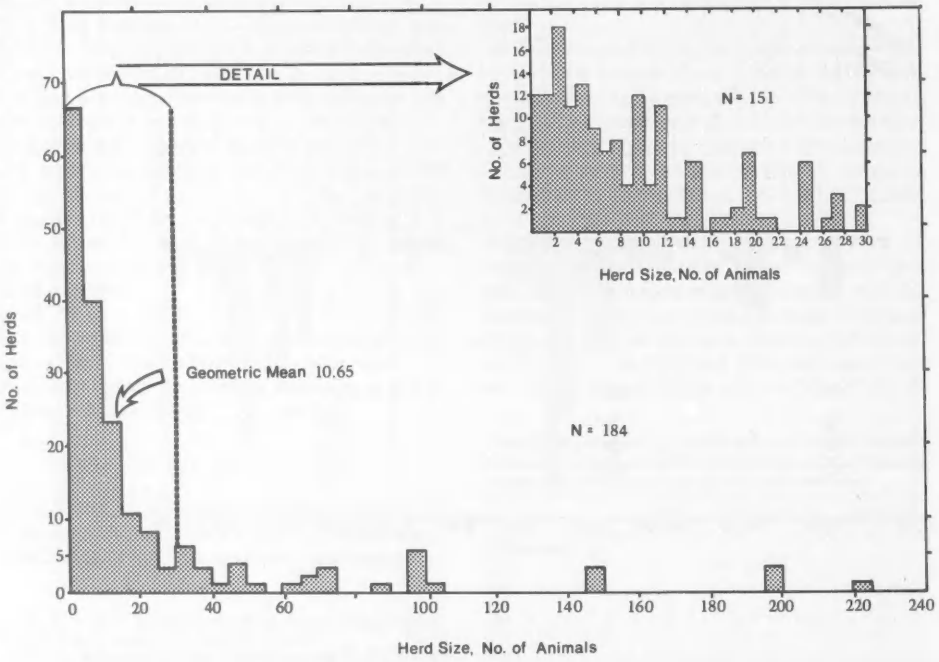

FIGURE 7.—Distribution of estimated "herd" sizes of Risso's dolphins, in the eastern North Pacific (1958-75). Inset gives detail for herd sizes with <30 animals.

The rather dramatic decrease in the number of sightings north of about lat. 13° N and the very limited number of offshore sightings in the broad belt from about the latitudes of Cedros and Guadalupe Islands south to approximately Acapulco, appear to reflect an area of apparent very low density in the species' distribution, since survey effort in the area was heavy even where no sightings were reported. Pronounced distributional gaps in portions of the same ocean area have been documented for *Delphinus delphis* (Evans 1975) and *Stenella* spp. (Perrin 1975).

Risso's dolphins appear to occur year-round in offshore waters from about central Baja California northward to about San Francisco. Movements onto the continental shelf of southern California are seasonal and appear to be related to surface temperatures. For example, records of Risso's dolphins over the continental shelf were more numerous in 1974 than in previous years since 1968, despite an equal effort, and more numerous than in 1975, despite increased survey effort in that year. In 1974 and 1975, surface temperatures were unusually high (California Cooperative Oceanic Fisheries Investigations[19]).

A poorly defined area of apparent low density in distribution, centering at about lat. 43° N, probably reflects generally poor sampling in the area from about San Francisco north to the latitude of Seattle and not any real change in the species' density there.

Records from lat. 45° to 51° N are most abundant during summer and are primarily off the continental shelf. Like the movements onto the southern California continental borderland and those into more northern latitudes, this change appears to relate to warming of surface waters.

The reports of abundance near Monterey in the late 19th century seem inconsistent with modern records of low abundance in the area. It may well be that this indication of the common occurrence of the species in Monterey Bay in the 1870's and 1880's represents a holdover of the occurrence of tropical animals in central California in the 1850's (Hubbs 1948). This being the case, the movement of Risso's dolphins north and inshore in some abundance during that period is consistent with behavior in 1974 and 1975 off southern California. Southward movements of the Dall's porpoise, *Phocoenoides dalli*, into southern California (Norris and Prescott 1961) and seasonal movements of the right whale dolphin, *Lissodelphis borealis* (Leatherwood and Walker 1979), and the Pacific whitesided dolphin, *Lagenorhynchus obliquidens* (Leatherwood and Reeves 1978), in the eastern North Pacific have been similarly linked to seasonal changes in water temperature.

Despite extensive survey effort in the northern temperate and Arctic eastern Pacific, Risso's dolphins have not been reported north of lat. 51° N. Therefore, since it provided no new data, the summary report of the species' occurrence in the Bering Sea (Clark 1945) is of doubtful accuracy.

Considered together, these records tend to support Davies' (1963) summary of the species' distribution, at least in the northeast Pacific. It appears, as he contended, to be primarily tropical, extending its range poleward to overlap with temperate forms, though not penetrating as far into high latitudes. Perhaps the most important point supported by these records is the dynamic nature of distribution of this (and probably other) marine mammal species. In addition to well-documented short-term and seasonal movements, there appears to have been a long-term fluctuation in the boundries of species' ranges, apparently in responses to long-term environmental changes.

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[19]California Cooperative Oceanic Fisheries Investigations. Unpublished data in files of CalCOFI at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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DESCRIPTION OF LARVAL AND JUVENILE RED SNAPPER, *LUTJANUS CAMPECHANUS*[1]

L. ALAN COLLINS, JOHN H. FINUCANE, AND LYMAN E. BARGER[2]

ABSTRACT

Identification and description of the red snapper, *Lutjanus campechanus*, family Lutijanidae, were based upon the general morphology, meristic characters, head spination, and pigmentation of 18 larval and 6 juvenile specimens, 4.0-22.4 mm standard length. These 24 specimens were selected from a total of 226 larval and juvenile *L. campechanus* which were collected mainly along the Texas coast from 1975 to 1977. Lutjanids <4.0 mm lacked presently recognizable characters that are diagnostic at the species level. The key to the development of the series was a unique meristic count. Some other useful diagnostic characters were: small serrations on the anterior margin of the pelvic spine in specimens of 4.8-12.4 mm, and a long unbroken soft ray immediately adjacent to the pelvic spine in specimens of 4.8-10.6 mm. A brief comparison was made between *L. campechanus* and other lutjanid larvae and juveniles.

The red snapper, *Lutjanus campechanus* (Poey), family Lutjanidae, is one of the most important commercial and recreational fish species in the Gulf of Mexico (Bradley and Bryan 1975; Beaumariage and Bullock 1976). Numerous biological and fisheries publications concern the adult of this species. Apparantly only one short publication has dealt with the early life history of *L. campechanus* however. Arnold et al. (1978) described the spawning of this species in captivity. The primary purpose of the present paper is to describe the larval and juvenile development of *L. campechanus*.

METHODS

A total of 226 larvae and juveniles (4.0-22.4 mm SL, standard length) of the species were captured by four different methods, which are listed in Table 1. The bongo and neuston net sampling was done according to Marine Resources Monitoring, Assessment and Prediction specifications (Jossi et al. 1975) and was made at a vessel speed of 2.8 km/h (1.5 kn).

The largest specimen was preserved in 40% isopropyl alcohol. Other larvae and juveniles were preserved in buffered 5% Formalin.[3] Some larval and juvenile specimens were stained with alizarin-red to aid in measuring and in counting body parts.

A dissecting microscope with an ocular micrometer was used to make standard measurements (Laroche 1977) on 24 specimens. The level of accuracy for micrometer measurements was 0.01 mm for measurements <1 mm and 0.1 mm for measurements >1 mm. All measurements of body length refer to standard length unless otherwise noted. Standard length was defined as the distance from the tip of the snout to the posterior tip of the notochord (before hypural formation) and the tip of the snout to the posterior margin of the hypurals (after hypural formation posterior to the notochord tip).

Larvae were defined as individuals which had absorbed the yolk sac but which had not completed differentiation of adult fin spine and ray complements. Juveniles were defined as sexually immature individuals having adult fin complements of spines and rays.

We used the serial or dynamic method of tracing certain characters back from juvenile to larval specimens (Moser and Ahlstrom 1970).

IDENTIFICATION

The genus *Lutjanus* is the most speciose in the family Lutjanidae. *Lutjanus campechanus* is 1 of 10 species of that genus which occur in U.S. waters <200 m deep (Bailey et al. 1970). *Lutjanus campechanus* occurs along the continental shelf of the

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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TABLE 1.—Catch data arranged chronologically for larval and juvenile *Lutjanus campechanus* from the Gulf of Mexico and adjacent waters.

Location	Depth range (m)	Latitude (N)		Longitude (W)	Period	Gear/tow	No. collected	Size (mm SL)	Temp. (° C)	Salinity (‰)
St. Andrew Bay, Fla.	6	30°09′		85°41′	July 1973	10.7 headrope otter trawl: 2.5 cm stretched mesh in cod end/bottom tow	1	22.4	27.0	33.7
South Texas continental shelf	42-131	27°54′	to	96°19′	Sept. 1975	1 m diameter plankton net: 0.250 mm mesh/ single oblique tow	59	4.0-12.4	19.7-29.2	33.7-36.4
		26°57′	to	96°48′						
		27°17′	to	96°23′						
		26°10′		96°24′						
	42-183	27°54′	to	96°19′	July-Sept. 1976	61 cm diameter bongo nets: 0.505, 0.333 mm mesh/double oblique tow	57	4.1-10.6	17.4-29.7	34.7-37.5
		26°57′	to	96°48′						
		27°15′	to	96°18′						
		26°10′		96°39′						
	49-131	27°30′	to	96°44′	May, July-Sept., Nov. 1977	As above	17	4.2-5.8	17.3-29.8	33.4-36.5
		27°17′	to	96°23′						
		26°10′		96°24′						
Buccaneer Oil Field, near Galveston, Tex.	17	28°52′		94°40′	July 1977	As above, also 1.0 × 0.5 m, 0.505 mm mesh neuston net	92	4.0-7.3	23.0-26.0	32.8-35.5

Atlantic coast of the United States and in the Gulf of Mexico (Rivas 1966). The taxonomy of this species has undergone several revisions. Three specific names have been used for the Gulf of Mexico red snapper in recent literature: *L. campechanus, L. aya,* and *L. blackfordii* (Anderson 1967). We used the American Fisheries Society (Bailey et al. 1970) nomenclature.

To date, the only lutjanid that has had its larval stages described in the literature is *Rhomboplites aurorubens* (Laroche 1977). Identification of lutjanid larvae is difficult unless a series of the larvae and juveniles is available for study.

Juveniles of only three Atlantic species of *Lutjanus* and one specimen of *Symphysanodon* have been illustrated. Illustrations of 10.5, 14.4, 19.9, and 48.5 mm juvenile *L. griseus* have been presented by Starck (1971). A 17.8 mm *L. synagris* or *L. mahogoni* was described and partially sketched by Heemstra (1974). A 14.4 mm fork length juvenile identified as *Lutjanus* sp. was illustrated by Fahay (1975). A 20 mm juvenile *Symphysanodon* was partially illustrated in Fourmanoir (1973).

Identification of the present series of *L. campechanus* is based upon the meristic characters of the juveniles. Six juveniles (8.0-22.4 mm) had the meristic complement of adult *L. campechanus* and formed the key to the series. These counts included 24 myomeres; X, 14 dorsal fin spines and rays; III, 9 anal fin spines and rays; 9 + 8 principal caudal fin rays; 16-18 pectoral fin rays; I, 5 pelvic fin spine and rays. These counts have also been reported for *L. analis* and *L. aya* (Miller and Jorgenson 1973). However, Anderson (1967) reported that *L. analis* has a maximum of 8 anal fin soft rays. Rivas (1966) reviewed the *L. campechanus* complex of "red snappers" and stated that the species described as *Bodianus aya* by Bloch in 1790 was probably not a lutjanid. Rivas recognized only two species in the complex commonly referred to as red snappers: *L. campechanus,* from the Gulf of Mexico and the South Atlantic coast of the United States, and *L. purpureus,* from the Caribbean Sea and southeastward along the coast of the Guianas, and probably to Brazil. Rivas (1966) synonymized *L. blackfordii* with *L. campechanus*. Therefore, *L. campechanus* is the only species occurring in the northern Gulf of Mexico which has the meristic complements observed in our specimens.

DESCRIPTION

Although we collected many lutjanid larvae, only those ≥4.0 mm were identifiable as *L. campechanus*. Lutjanids <4.0 mm lacked presently recognizable characters diagnostic at the species level and, therefore, were not described. This gen-

eral lack of development has also been observed in laboratory-reared larvae of *L. campechanus* <4.0 mm (Rabalais[4]).

Pigmentation

Diagnostic melanophores occurred on various regions of the specimens (Table 2). The first melanophore to appear on the head was on the dorsal midline over the midbrain. The dorsal surface of the peritoneum was nearly covered by large melanophores in all specimens. The presence and amount of pelvic fin pigment was variable. Fading of the pigment in some specimens was probably due to the preservation and/or handling. When pelvic fin pigment was present in specimens <7.3 mm, it was located only on the fin membrane. Our undamaged specimens ≥7.3 mm had pelvic fin melanophores primarily on the most anterior soft ray (Figure 1D) and/or in the fin membrane (Figure 2B).

The largest juvenile had the most pigmentation (Figure 2C). Four vertical bars made up of small melanophores were located between the head and the caudal section. All fin membranes between the 2d and 10th posteriormost spinous dorsal rays had three melanophores between each spionous ray. The soft dorsal fin had five melanophores on the fin membranes between the 7th and 13th posteriormost rays. An additional melanophore was present near the distal end of the dorsal principal caudal rays. Unfortunately, specimens were not available to link the development of pigmentation between 12.4 and 22.4.

Fin Formation

Dorsal and pelvic fins were the first to begin development in *L. campechanus* (Figure 1A), followed by caudal, anal, and pectoral fins. The adult complement of fin spines and rays was completed in the following order: caudal (principal rays only), pelvic, pectoral, dorsal, and anal (Table 3).

Dorsal Fin

The smallest illustrated specimen had developed only the five anteriormost dorsal spinous rays (Figure 1A). Most dorsal soft rays seemed to develop simultaneously, with the exception of the posteriormost soft rays which developed last. The total adult number of dorsal fin rays (24) was present at 4.9 mm, with the 2 posteriormost dorsal

[4]N. Rabalais, University of Texas Marine Laboratory, Port Aransas, TX 78373, pers. commun. October 1978.

TABLE 2.—Number of melanophores on regions of larval and juvenile *Lutjanus campechanus*. When available, several larvae of a given size were used in determining the number of melanophores.

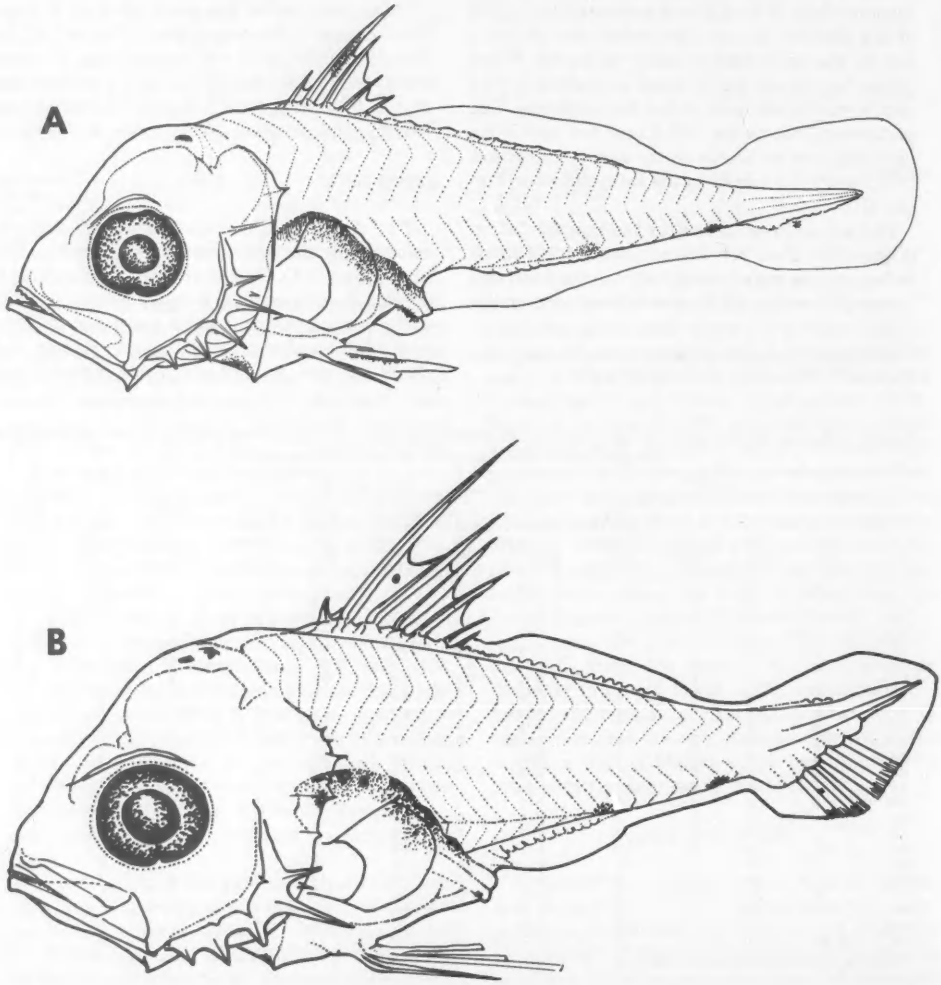
	Head				Gut		Dorsal and pelvic		Caudal			
SL (mm)	Over fore-brain	Over mid-brain	On oper-culum	On ventral midline anterior to ventral tip of cleithrum	Internal, over dorsal surfaces of peritoneum	On ventral midline just anterior to anus	Fin membrane between 2d and 3d dorsal spines	On anterior portion of pelvic fin	Internal, near posterior base of anal fin	On ventral midline of myomere no. 22-25	On ventral principal caudal rays	Internal, lateral to notochord and anterior to point of flexion
4.0	0	1	0	1	5-10	1	1-2	1-2	1	1	1	0
4.2	0	1-2	0	1	5-10	1	1-2	0-2	1	1	1	0
4.6	0	1	0	1	5-10	1	2	0-2	1	1	1	0
4.7	0	2	0	1	5-10	1	2	0-2	1	1	1	0
4.8	0	2	0	1	5-10	1	3-7	1-2	1	1	1	0
4.9	0	1-2	0	1	5-15	0-1	3-6	0-2	1	1	1	0
5.4	0	1	0	1	5-15	0-1	1-8	0-1	1	1	1	0
5.5	0	1-2	0	1	5-15	0	3-5	0-3	1	1	1	0
6.1	0	2-3	0	1	5-15	0	2-8	2-3	1	1	1	0-1
6.2	0	3-5	0	1	5-15	0	3-8	1-2	1	1	1	0-1
6.3	0	1-2	0	1	5-15	0	3-8	1-2	1	1	1	0-1
6.4	0	1-6	0	1	5-15	0	3-8	0-2	1	1	1	0-1
6.5	0	1-3	0	1	5-15	0	3-8	1-3	1	1	1	(1)
6.6	0	3-4	0	1	5-15	0	1-8	0-8	1	1	1	0-1
7.3	0	2	0	1	5-15	0	12-20	14	1	1	1	1
7.4	1	6	2	1	5-15	0	2	(1)	1	1	1	1
7.5	3	9	2	1	5-15	0	1	3	1	1	1	1
7.6	(1)	(1)	(1)	(1)	5-15	0	3-8	(1)	1	1	1	1
[2]8.0	1	13	1	1	5-15	0	3	(1)	1	1	1	1
[2]9.0	3	17	2	0	5-15	0	3-8	(1)	1	1	1	1
[2]9.5	6	30	2	0	5-15	0	3-8	3-8	1	1	1	1
[2]10.6	3	34	3	0	5-15	0	3-8	3-8	1	1	1	1
[2]12.4	7	36	1	0	5-15	0	10	6	1	1	1	1
[2]22.4	ca. 30	ca. 100	2	0	ca. 20	0	3	(1)	1	3	4	2

[1]Specimen was damaged and no count was taken.
[2]Juvenile.

spines represented by 2 soft rays (Table 3). At 5.4 mm the anteriormost soft ray became a spine. All specimens ≥7.5 mm had X, 14 dorsal fin spines and rays. The second dorsal spine was the longest ray in the dorsal fin in specimens 4.0-12.4 mm. In the 22.4 mm specimen, all dorsal fin rays except the first spine were about equal in length (Figure 2C). Serrations did not appear on the dorsal spines of *L. campechanus* between 4.0 and 22.4 mm.

Pelvic Fin

The smallest larva had not yet developed pelvic fin soft rays but had developed the pelvic spine (Figure 1A). The pelvic spine was smooth on the anterior margin on 4.0 and 4.7 mm specimens. Between 4.7 and 4.8 mm this spine developed ~30 fine serrations along its anterior margin. All larvae and juveniles 4.8-12.4 mm had these serrations. The number of serrations generally in-



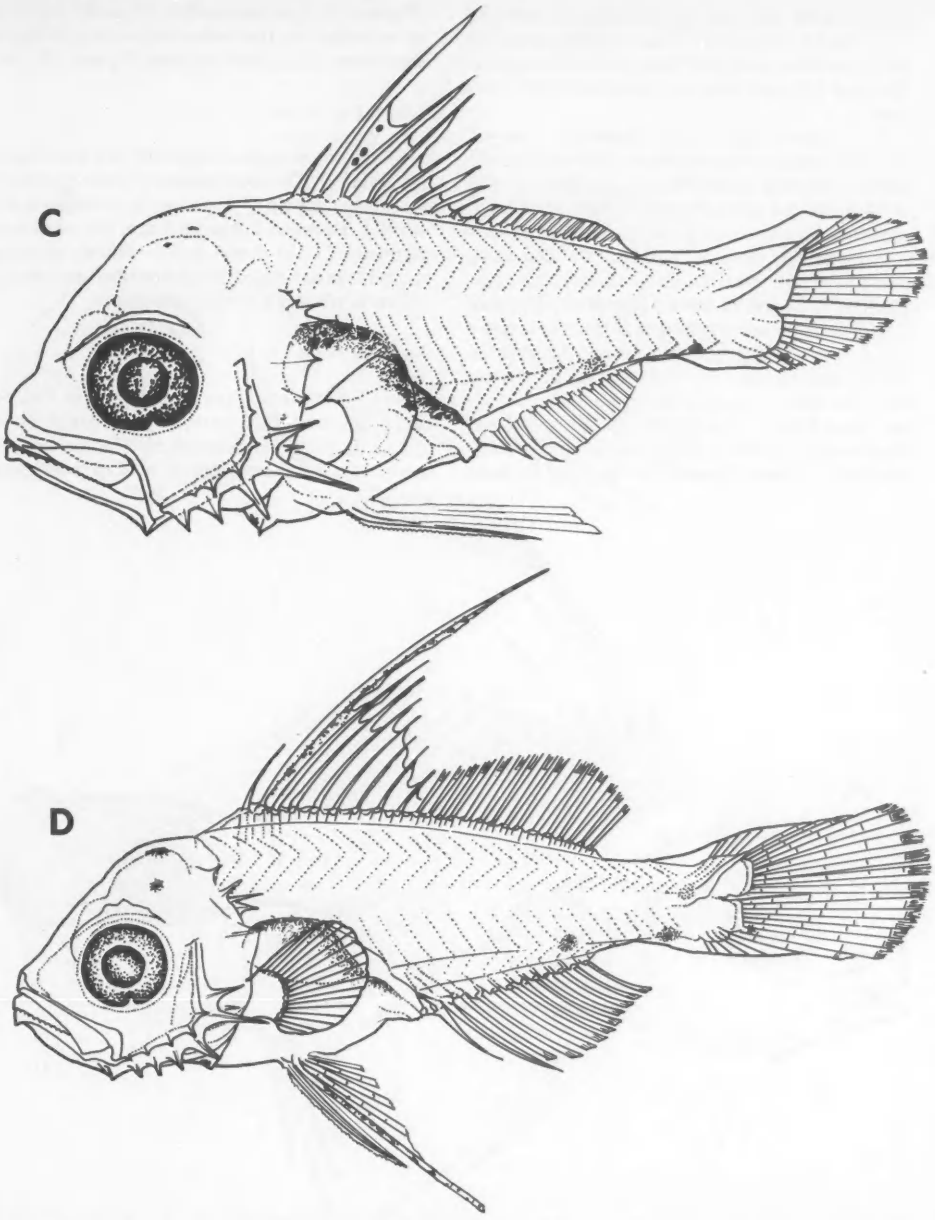


FIGURE 1.—Developmental stages of the red snapper, *Lutjanus campechanus*, larvae drawn using a camera lucida: A, 4.0 mm SL; B, 4.2 mm; C, 4.9 mm; D, 7.3 mm.

creased with specimen size between 4.8 and 12.4 mm. The 12.4 mm juvenile had ~60 fine serrations on the anterior margin of each of its pelvic spines. Between 12.4 and 22.4 mm these serrations were lost.

Three distinct pelvic rays appeared on the 4.2 mm larva in the anterior portion of the previously undifferentiated finfold (Figure 1B). Between 4.6 and 5.5 mm the pelvic fin attained the adult complement of 1 spine and 5 soft rays (Table 3).

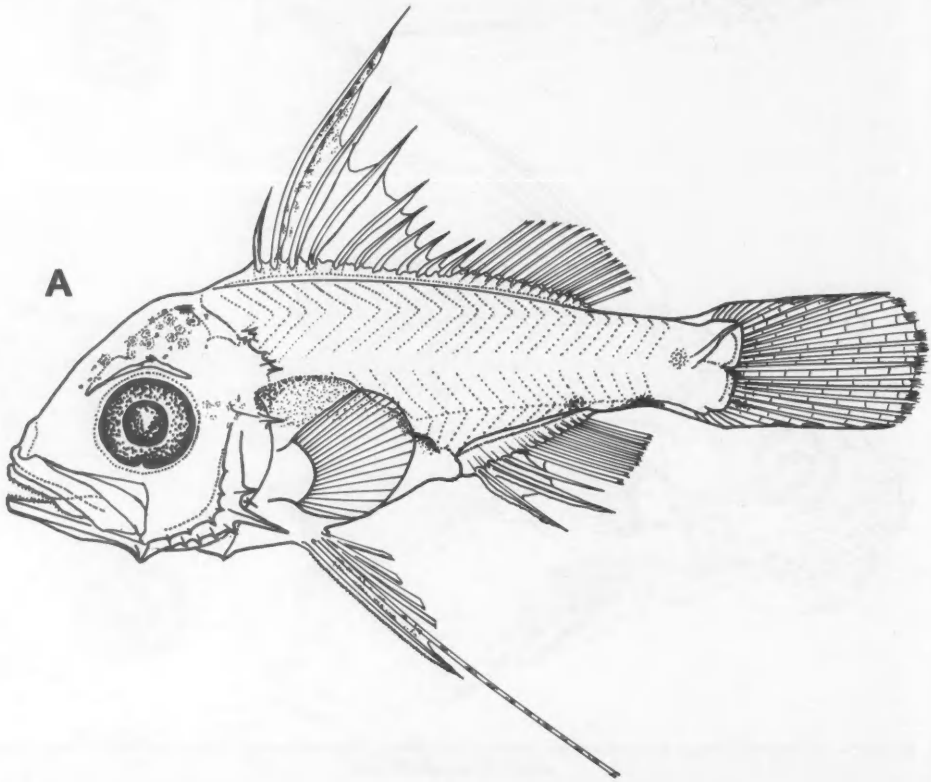
The pelvic spine was long. It extended to or beyond the anus in all but the smallest and largest specimens, 4.0 and 22.4 mm, respectively (Figures 1, 2). The pelvic soft ray closest to the pelvic spine was always the longest pelvic fin ray. Apparently this longest ray may be easily broken off during collection and handling. Approximately half of all specimens had this ray broken off. The unbroken, anteriormost pelvic ray in specimens 4.8-10.6 mm extended at least to the center of the anal fin base (Figure 1C). Specimens of 6.4, 7.3, and 9.5 mm had an unbroken ray that extended posteriorly beyond the center of the anal fin base (Figures 1D, 2A).

Caudal Fin

Caudal fin formation began at ~4.2 mm (Figure 1B, Table 3). The most ventral principal rays and those near the tip of the urostyle were the last to develop. Between 4.2 and 4.7 mm the adult complement of 17 (9 dorsal and 8 ventral) principal caudal rays developed. Notochord flexure occurred between 4.7 and 4.9 mm (Table 3).

Anal Fin

At 4.7 mm, 8 anal rays were present as 2 spines and 6 soft rays in the anteriormost part of the fin (Table 3). The posteriormost rays formed last. By 4.9 mm the adult complement of 12 rays was pres-



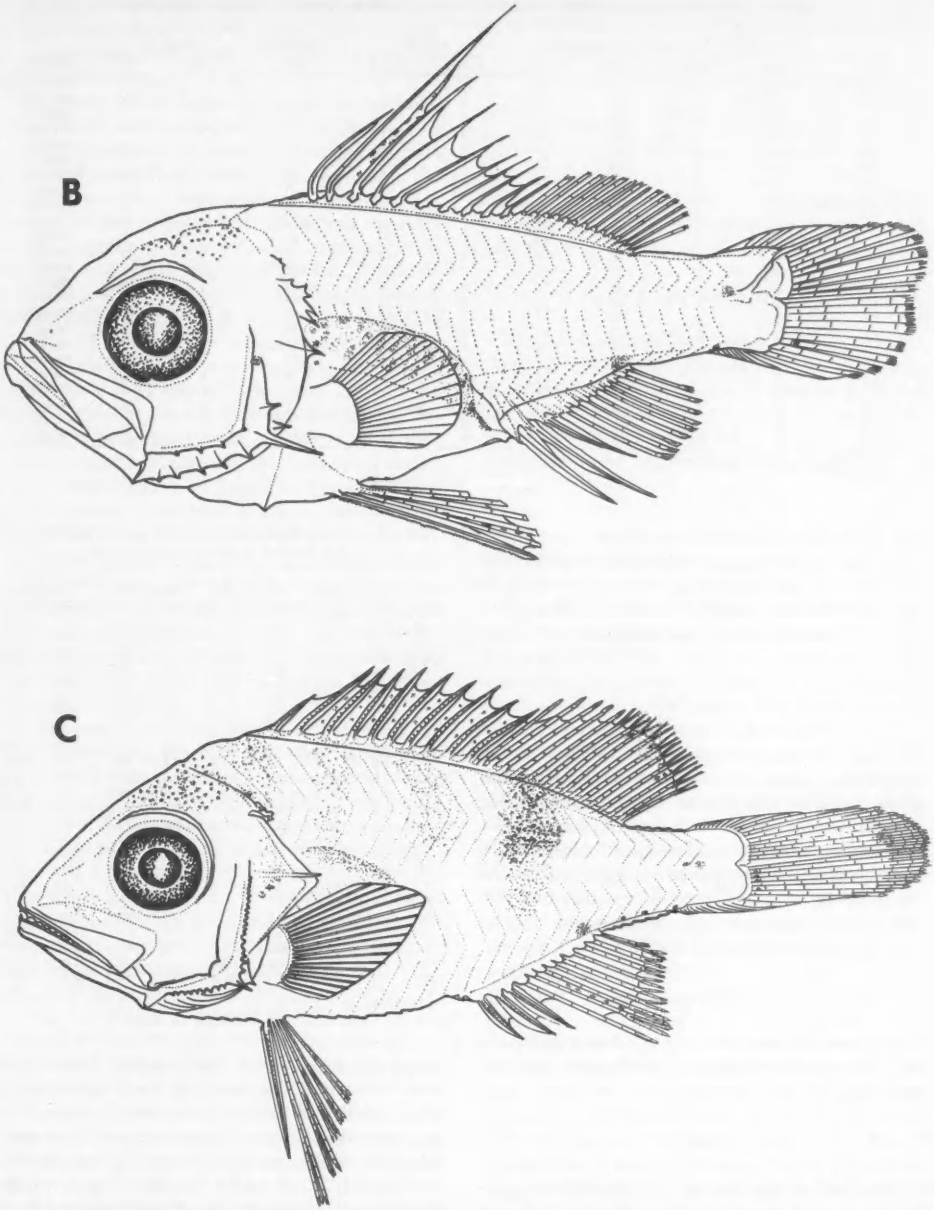


FIGURE 2.—Developmental stages of the red snapper, *Lutjanus campechanus*, juveniles drawn using a camera lucida: A, 9.5 mm SL; B, 12.4 mm; C, 22.4 mm.

TABLE 3.—Meristic characters and notochord flexure of larval and juvenile *Lutjanus campechanus*.

SL (mm)	Principal caudal fin rays		Dorsal fin		Anal fin		Pectoral fin	Pelvic fin		Notochord
	Upper	Lower	Spines	Rays	Spines	Rays	Rays	Spines	Rays	
4.0	0	0	V	0	0	0	0	I	0	Straight
4.2	4	4	VII	0	0	0	(1)	I	3	Straight
4.6	5	5	VI	0	0	0	(1)	I	3	Straight
4.7	9	8	VII	8	II	6	(1)	I	4	Flexed
4.8	9	8	VIII	11	II	8	(1)	I	4	Straight
4.9	9	8	VIII	16	II	10	(1)	I	(1)	Flexed
5.4	9	8	IX	15	II	10	(1)	I	(1)	Flexed
5.5	9	8	IX	15	II	10	(1)	I	5	Flexed
6.1	9	8	IX	15	II	10	(1)	I	5	Flexed
6.2	9	8	IX	15	II	10	(1)	I	5	Flexed
6.3	9	8	IX	15	II	10	(1)	I	5	Flexed
6.4	9	8	IX	15	II	10	(1)	I	5	Flexed
6.5	9	8	IX	15	II	(1)	(1)	I	5	Flexed
6.6	9	8	IX	15	II	10	14	I	5	Flexed
7.3	9	8	IX	15	II	10	16	I	5	Flexed
7.4	9	8	IX	15	II	10	17	I	5	Flexed
7.5	9	8	X	14	II	(1)	16	I	5	Flexed
7.6	9	8	X	14	II	10	17	I	5	Flexed
[2]8.0	9	8	X	14	III	9	17	I	5	Flexed
[2]9.0	9	8	X	14	III	9	18	I	5	Flexed
[2]9.5	9	8	X	14	III	9	18	I	5	Flexed
[2]10.6	9	8	X	14	III	9	18	I	5	Flexed
[2]12.4	9	8	X	14	III	9	18	I	5	Flexed
[2]22.4	9	8	X	14	III	9	17	I	5	Flexed

[1]An accurate count was not possible.
[2]Juvenile

ent in the form of 2 spines and 10 soft rays (Figure 1C). The transformation of the anteriormost soft ray into the third anal spine occurred between 7.6 and 8.0 mm and marked the end of the larval period. Anal spines were not serrated.

Pectoral Fin

The 4.0 mm larva had only a pectoral finfold (Figure 1A). Between 4.0 and 6.5 mm ray development began, but ossification was not completed and the exact number of rays was difficult to determine. The 6.6 mm larva had 14 pectoral rays, and 2 more rays were added by 7.3 mm. The 16 rays on the 7.3 mm specimen were within the 16-18 range for adult pectoral rays (Rivas 1966). The number of pectoral rays on specimens 7.3-22.4 mm varied from 16 to 18 (Table 3).

Squamation

Scales were present on the 22.4 mm specimen only. An accurate lateral line scale count was not possible.

Head

The head of the larval and juvenile *L. campechanus* was large, ranging between 32.5 and 44.9% SL (Table 4). Head size (head length as percent of SL) generally increased in larvae and decreased in juveniles. The smallest and largest specimens had the smallest head proportions, 32.5% on the 4.0 mm larva and 34.8% on the 22.4 mm juvenile. The head was proportionally largest, 44.9 and 44.4%, on the 4.9 and 5.4 mm larvae, respectively. Head length was about equal to body depth in all specimens. Head length ranged from 32.5 to 44.9% SL and body depth from 32.5 to 43.9% SL.

TABLE 4.—Measurements and body part proportions for larval and juvenile *Lutjanus campechanus*.

SL (mm)	Head length		Snout to anus length		Body depth		Eye diameter	
	(mm)	(% SL)	(mm)	(% SL)	(mm)	(% SL)	(mm)	(% SL)
4.0	1.3	32.5	1.9	47.5	1.3	32.5	0.44	11.0
4.2	1.6	38.1	2.3	54.8	1.5	35.7	0.51	12.1
4.6	1.7	37.0	2.3	50.0	1.5	32.6	0.53	11.5
4.7	1.9	40.4	2.6	55.3	1.8	38.3	0.59	12.6
4.8	1.8	37.5	2.8	58.3	1.9	40.0	0.66	13.8
4.9	2.2	44.9	3.0	61.2	2.0	40.8	0.56	11.4
5.4	2.4	44.4	3.3	61.1	2.3	42.6	0.77	14.3
5.5	2.3	41.8	3.4	61.8	2.1	38.2	0.70	12.7
6.1	2.4	39.3	3.6	59.0	2.3	37.7	0.78	12.8
6.2	2.6	41.9	3.9	62.9	2.4	38.7	0.79	12.7
6.3	2.6	41.3	3.8	60.3	2.5	39.7	0.79	12.5
6.4	2.4	37.5	3.8	59.4	2.6	40.6	0.79	12.3
6.5	2.6	40.0	4.1	63.1	2.7	41.5	0.83	12.8
6.6	2.8	42.4	4.3	65.1	2.9	43.9	0.87	13.2
7.3	2.7	37.0	4.3	58.9	2.8	38.4	0.95	13.0
7.4	3.1	41.9	4.7	63.5	3.1	41.9	0.93	12.6
7.5	3.0	40.0	4.7	62.7	3.1	41.3	0.97	12.9
7.6	3.1	40.8	4.7	61.8	3.0	39.5	0.98	12.9
[1]8.0	3.2	40.0	5.1	63.8	3.3	41.3	0.99	12.4
[1]9.0	3.3	36.7	5.8	64.4	3.3	36.7	1.2	13.3
[1]9.5	3.5	36.8	5.9	62.1	3.4	35.8	1.2	12.6
[1]10.6	4.0	37.7	6.7	63.2	4.0	37.7	1.2	11.3
[1]12.4	4.8	38.7	7.9	63.7	4.7	37.9	1.4	11.3
[1]22.4	7.8	34.8	15.1	67.4	8.1	36.2	2.7	12.1

[1]Juvenile.

Spines were found on the preopercle, posterodorsal margin of the operculum, posttemporal, and supracleithrum. Serrations developed on the supraocular crest.

The preopercular spines developed in two rows, one anterior to the preopercular margin and one along the preopercular margin (Figures 1, 2). Both rows had vertical and horizontal segments. The vertical segments were situated approximately perpendicular to the body midline, and the horizontal segments were situated approximately parallel to the body midline of the fish. The anteriormost row had 3-6 spines (1-3 vertically and 2-3 horizontally) in the 4.0-22.4 mm specimens. The number of anterior row spines decreased in the largest specimens. The row along the preopercular margin had 5-27 spines (2-18 vertically and 3-9 horizontally) in the 4.0-22.4 mm specimens. The number of both vertical and horizontal preopercular margin spines increased between 12.4 and 22.4 mm. Vertical spines increased by 16 and horizontal spines increased by 4 along the preopercular margin between these two lengths.

A small spine was present on the interopercle of all specimens. A larger spine was also present on the posterodorsal margin of the opercle of all specimens. (Figures 1, 2). The spine at the angle of the preopercle was the largest spine on the head. No serrations developed on this or any other preopercular spine.

A spine on the posttemporal was first present on the 7.3 mm larva. A second spine developed on this bone by 9.5 mm. These 2 posttemporal spines were greatly reduced in the two largest specimens. A supracleithral spine was present on the smallest larva (4.0 mm). Three spines were present by 4.2 mm, and 5 spines had developed by 9.5 mm (Figures 1A, B; 2A). The 2 most ventral supracleithral spines were longer in the 12.4 mm specimen than in smaller specimens. The 22.4 mm juvenile had all of the supracleithral spines, but these spines were much smaller (Figure 2C).

Two serrations developed on the supraocular crest by 7.3 mm (Figure 1D), and two more by 12.4 mm. The 22.4 specimen had no serrations on the supraocular crest (Figure 2C).

Eye diameter was 11.0-14.3% SL (Table 4). The eye was almost spherical, and the iris had a ventral cleft in all but the largest specimen (Figures 1, 2).

Teeth were present in all specimens on the dentary and premaxillary bones. In addition, the two largest specimens (12.4 and 22.4 mm) had vomerine and palatine teeth. The vomerine teeth in these two specimens were arranged in a V-shaped pattern with the angle pointed anteriorly.

TABLE 5.—Predictive linear regressions of body measurements on standard length for 24 larval and juvenile *Lutjanus campechanus* over the size range 4.0-22.4 mm SL.

Measurement	Slope	Intercept	$S_{y \cdot x}$	r
Head length	0.341	0.350	0.177	0.991
Body depth	0.699	-0.601	0.159	0.998
Snout to anus length	0.359	0.197	0.181	0.992
Eye diameter	0.118	0.050	0.054	0.993

Body Growth

Measurements of four body parts are given in Table 4. The growth of these parts in relation to standard length is described by linear regressions (Laroche 1977; Sokal and Rohlf 1969), the statistics for which are presented in Table 5. All relationships have high correlation coefficients of ≥0.991.

Comparison With Other Lutjanid Larvae and Juveniles

As stated earlier, *R. aurorubens* is the only lutjanid to have previously had its larval and juvenile stages described. The two snappers are easily separated as follows: In specimens ≥4.0 mm, *R. aurorubens* has serrations on the largest spine at the preopercular angle. Figure 1A in Laroche (1977) did not show the serrations on this spine, however, the text stated that, "A large, stout, and serrated spine occurs at the preopercular angle in all specimens." Laroche[5] confirmed this. In addition, large serrations develop on the anterior and posterior margins of the dorsal and pelvic spines in larval *R. aurorubens* ≥4.7 mm. None of the 4.0-4.7 mm *L. campechanus* had serrated preopercular, dorsal, or pelvic spines. Both species have serrated pelvic spines in specimens >4.8 mm, but *R. aurorubens* has large serrations on the anterior and posterior margins while *L. campechanus* has small serrations on just the anterior margin. The total number of rays in the dorsal and anal fins also separates these two snappers at sizes ≥5.0 mm. *Rhomboplites aurorubens* has 22 or 23 dorsal and 11 anal rays while *L. campechanus* has 24 dorsal and 12 anal rays. *Rhomboplites aurorubens* is the only lutjanid to have an adult complement of

[5]W. A. Laroche, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. June 1978.

12 dorsal spines. All other members of the Lutjanidae have 10 spines. Finally, the head length of *R. aurorubens* is greater than the body depth (Laroche 1977), while in *L. campechanus* head length is about equal to body depth (Table 4).

Identification of the larvae and juveniles of other lutjanid species is more difficult than that of *L. campechanus* and *R. aurorubens*, since the meristic characters are very similar in most other species of lutjanids. At the present time, field-collected lutjanid larvae <4.0 mm can be identified only to family. Laboratory rearing presents the most likely solution to the larval and juvenile lutjanid taxonomic problem.

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ISOLATION OF OLIVE ROCKFISH, *SEBASTES SERRANOIDES*, POPULATIONS OFF SOUTHERN CALIFORNIA

MILTON S. LOVE[1]

ABSTRACT

Movements of the olive rockfish, *Sebastes serranoides*, off Santa Barbara, California, were investigated, using mechanical and parasite tags. The movements were restricted over shallow reefs though somewhat less so around deeper oil platforms. Highly restricted movements may cause greater vulnerability of populations to overfishing—comparisons of olive rockfish size frequencies between two reefs indicated that fishing pressure had reduced olive rockfish populations to almost all prereproductive individuals on the more heavily fished site.

Rockfishes, genus *Sebastes* (Family Scorpaenidae), form a most diverse fish group along the California coast. Some 57 species are found in these waters (Miller and Lea 1972), inhabiting virtually every marine habitat from estuarine (occasionally) and intertidal waters to depths of more than 610 m (Miller and Lea). Rockfish are very important to both sport and commercial fishing industries; in California waters in 1974, rockfish ranked third in the commercial fishery (poundage landed) and first in the sport fishery (numbers landed) (McAllister 1976).

California species can be roughly divided into two bathymetric groups: shallow species that inhabit subtidal areas of reef and kelp, and those that live in relatively deep water (deeper than about 70 m). All species are ovoviviparous, producing pelagic larvae. There is some evidence that the shallow water species may remain within a relatively small area of reef or kelp (Miller and Geibel 1973).

A species that consists of relatively sedentary, reef-oriented aggregations would present potential problems in management, as certain management strategies presuppose movements of this fish (Harden Jones 1968; Cushing 1968). If the exploited species inhabits reefs, for example, it might soon be decimated at a heavily fished reef if individuals were parochial and did not move from an unexploited site to repopulate the depleted one. Obviously, a management strategy to protect this type of segregated reef species would differ from that for a species whose individuals move between sites. Many rockfish species grow very slowly (Phillips 1964; Chen 1971: Westrheim and Harling[2]). Thus, even if a depleted reef were densely settled by a successful year class, it would not harbor adults for a number of years. Before then, the subadults would probably be caught before the age of first maturity, so the reef would effectively be lost as a site of propagation for the species. If this process continued through all available reef sites, the fisheries would be endangered.

On the other hand, a rockfish species whose individuals move freely from reef to reef may be less vulnerable to such perturbations. Even a locally depleted reef could be sufficiently repopulated by adults during breeding season because of the typically high fecundity of females (Phillips 1964) and great dispersability of pelagic larvae. Thus the fishery might be effectively managed by conventional procedures of establishing catch limits, etc.

The olive rockfish, *Sebastes serranoides*, inhabits reefs and kelp beds from San Benito Island, Baja California, north to Redding Rock, Del Norte County, northern California, and from intertidal waters (juveniles) to 146 m (Miller and Lea 1972). The species is most common in southern and central California from surface waters to depths of about 75 m. It is a major sport fish throughout much of the state (Miller and Gotshall 1965), particularly in southern and central California. Objectives of the present study were to determine whether individuals move from reef to reef and if average size was smaller at heavily fished reefs.

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METHODS

Artificial Tagging

Between 26 October 1973 and 17 October 1976, 1,847 olive rockfish (19-43 cm total length, TL) were tagged and released upon capture at 18 sites off southern California (Figure 1, Table 1). Generally, sites were selected either on the basis that they were reefs regularly fished by partyboats or private vessels, which maximized the opportunity to recapture tagged animals; or that sites had to be within 2 km of another regularly fished reef that harbored olive rockfish, which maximized the opportunity to recover fish that move short distances. The exception was Naples Reef, which had no other suitable site within 2 km. Naples Reef was included because its fish fauna was being studied intensively by other scientists. Only a few fish were tagged at some sites, such as Anacapa Island, Platform Holly, and Avila, either because olive rockfish were infrequent there or because the sites were relatively remote from Santa Barbara.

The tags (yellow Floy[3] anchor type FD-67c) consisted of a plastic tube 42 mm long with a 15 mm nylon stem and a 10 mm cross bar attached to the stem and were inserted with a Floy tagging gun, FDM 68, with a heavy-duty needle 2 cm long. My name, Department of Biology, UCSB, and a number were printed on each tag. The anchor was injected into the dorsal musculature between the second and third dorsal spines, leaving the brightly colored end free. Even though bryozoan growth completely obscured the legend within a few months, this growth was easily rubbed off by a person's finger when the tag was read.

Fish were caught by hook and line aboard research vessels and sportfishing partyboats, then measured, tagged, and returned to the water. Because of expanded gas in their swim bladders, fish taken at depths greater than about 20 m had to be deflated before they could return to depth. Perhaps 10% of all fish tagged required deflation, using a technique modified slightly from Gotshall (1964). A 3.8 cm, 18 gage hypodermic needle was inserted through the body wall into the swim bladder. However, instead of placing both fish and needle underwater, then waiting for the gas bubbles to stop emanating from the needle, gas was sucked from the bladders to speed the process, and if needed, the fish's everted stomach was pushed back into place. About 20% of the inflated fishes died either before or immediately after being returned to the water. Undoubtedly others that swam downward also died; of six fish placed in a tank after deflation, two died within 1 day and the rest survived for 2 wk, to the end of the test. Eliminated were all fish whose eyes were everted by gas expansion in the choroid plexa. Experience with *S. caurinus*, *S. paucispinis*, and *S. serranoides* indicates that this condition frequently leads to blindness and/or death, whether or not pressure is released.

Tagging mortality in fish that did not have to be deflated was probably low. Ten of 12 tagged olive rockfish lived for 2 mo in an aquarium, two dying after about 1 mo, apparently of a fungal infection. I saw none of the extensive hemorrhaging previously observed in Floy-tagged Pacific mackerel, *Scomber japonicus* (Gregory[4]).

TABLE 1.—Descriptions and locations of tagging sites for olive rockfish near Santa Barbara, Calif. For locations of sites see Figure 1 also.

Site and description
Diablo Canyon, Avila—11 km west of Avila Harbor, 9 m reef in 33 m, 0.3 km offshore
Naples Reef—24 km west of Santa Barbara, 1.6 km offshore, in 8-10 m, surrounded by 16-20 m deep sand flats
Oil Platform Holly—18 km southwest of Santa Barbara, in 60 m, about 3.2 km offshore
1 Mile Reef—2 km southeast of Santa Barbara, 2-6 m reef in 30-35 m
Horseshoe Reef—10 km east of Santa Barbara. Average depth 8-10 m, surrounded by 12-13 m
Oil Platform Hilda—8.7 km east of Santa Barbara, 3.1 km offshore in 34 m
4 Mile Reef—6.4 km southeast of Santa Barbara, 6-8 m pinnacle in 40 m
Oil Platform Hillhouse—10.4 km southeast of Santa Barbara, 8.9 km offshore in 58 m
Oil Platforms Houchin, Hogan, Hope—About 14.0 km southeast of Santa Barbara, about 7 km offshore in 50 m
Talcott Shoals, Santa Rosa Island—64.0 km southwest of Santa Barbara, 2-15 m pinnacles in 4-45 m
Fraser Pt., Santa Cruz Island—46 km south of Santa Barbara, 2-6 m reefs in 12-15 m
Smugglers Cove, Santa Cruz Island—40 km southeast of Santa Barbara
Anacapa Island—43 km southeast of Santa Barbara
Rincon Oil Island—19 km east of Santa Barbara (not figured)
Deephole Reef—68 km east of Santa Barbara, 2-6 m reefs in 24-28 m, about 1.8 km offshore (not figured)

Biological Tagging

I analyzed the parasite mix of olive rockfish to determine the feasibility of using parasites as "biological tags." Differences in parasite infection

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]Gregory, P. A. 1977. Results of tagging mortality experiments on Pacific mackerel, *Pneumatophorus japonicus*. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 40, 21 p.

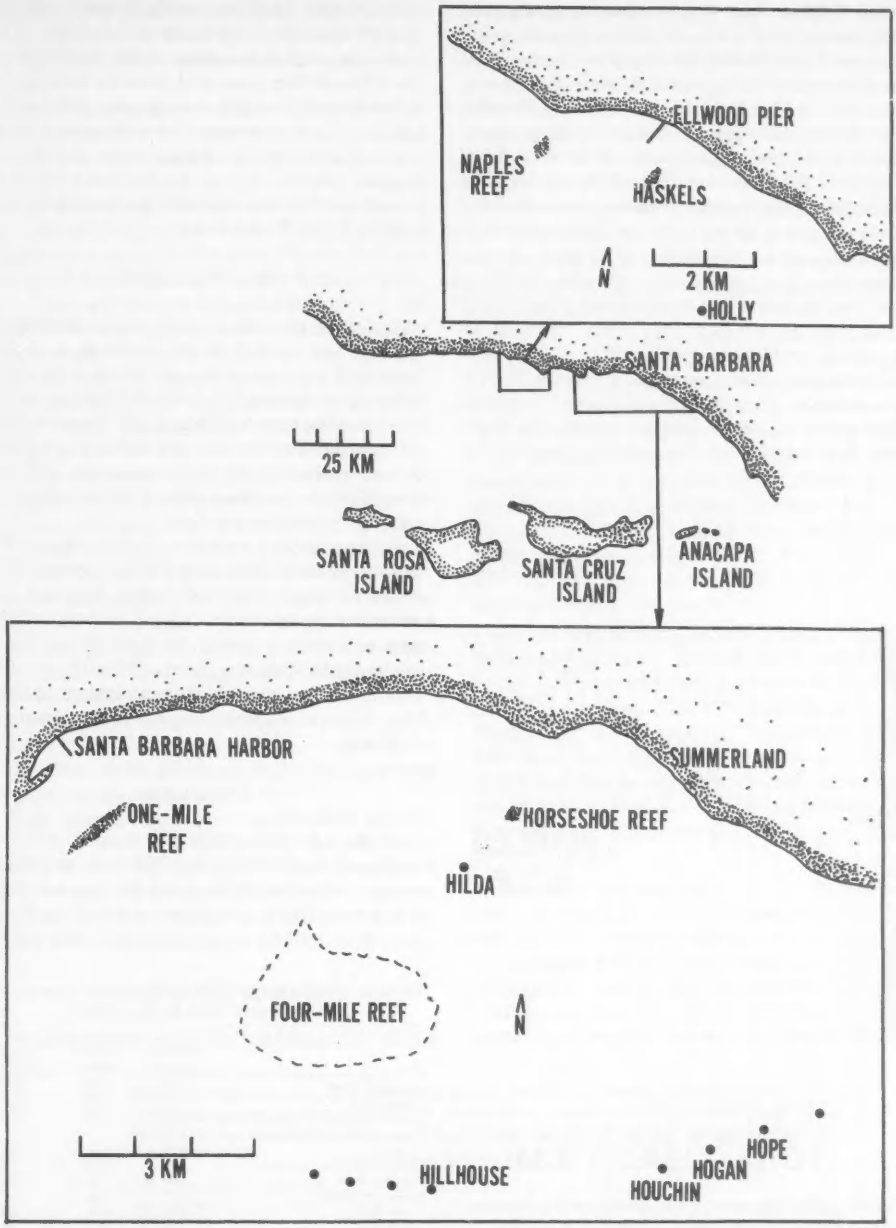

FIGURE 1.—Location of tagging and sampling sites for olive rockfish near Santa Barbara, Calif. Specific sites are described in Table 1. Deep Hole Reef (68.6 km east of Santa Barbara) and Rincon Oil Island (19 km east of Santa Barbara) are not included.

rates between host groups within a species can indicate reduced movement of fish between populations (Kabata 1963). Twenty olive rockfish from each of six sites (Naples Reef, Ellwood Pier, Horseshoe Reef, 4 Mile Reef, and oil platforms Houchin and Hillhouse—Figure 1) were sampled quarterly by hook and line or spear, between June 1976 and March 1977, placed on ice and frozen for later dissection. After thawing, fish were measured and were examined for parasites on the external surfaces as well as the gills, gill cavities, mouth, mesentery, heart, gallbladder, stomach, intestine, and muscle. Initially, copepods and monogenetic and digenetic trematodes were fixed in an alcohol-formaldehyde-acetic acid (AFA) solution and the trematodes were stained with Harris' hematoxylin, cleared with xylene, and mounted. Protozoans were studied unpreserved after thawing. Because most of the parasites recurred frequently, only those not readily indentifiable were preserved in the latter parts of the study.

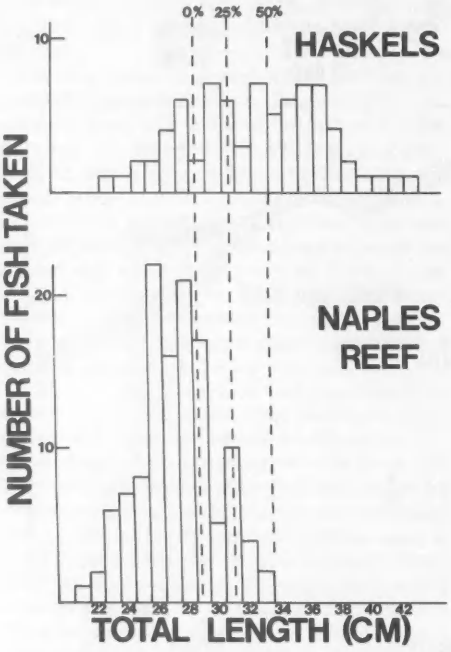

FIGURE 2.—Size frequencies of olive rockfish taken by partyboat at a heavily fished (Naples Reef) and lightly fished (Haskels) site (Naples Reef—N = 121, $\bar{x}$ = 27.3, SD = 2.5; Haskels—N = 76, $\bar{x}$ = 32.8, SD = 4.4). Dashed lines indicate size at which 0%, 25%, and 50% of the fish were mature.

After a year of sampling, it was apparent that the Ellwood Pier population was the only one not infected with the gill monogenean, *Microcotyle sebastis*. To test whether environmental conditions precluded *M. sebastis* from the site, 21 tagged, infected fish from the Horseshoe Reef were introduced into the Ellwood site. Specimens were collected after 1 and 6 mo.

Size Variation

To test whether heavy fishing pressure altered the size composition of olive rockfish on reefs, I compared size frequencies of fish taken by a sport fishing partyboat at Naples Reef (13 trips) and at a portion of the mainland bed called "Haskels" (four trips), which lies inshore and east of Naples Reef. A 4-yr study of partyboat operations indicated that Haskels had been fished by partyboats no more than four times in 5 yr.

Data on size and maturity of olive rockfish (Figure 2) was taken from Love (1978), who examined 365 individuals from off Santa Barbara. The gonads of mature olive rockfish undergo marked annual changes, similar to those in the Pacific ocean perch, *Sebastes alutus*, (Westrheim 1975) and mature individuals are readily distinguished from immature specimens, based on gonad size and color.

RESULTS

Of the 1,847 fish artificially tagged, 216 were recovered, an 11.2% return (Table 2), and 9 were recaptured twice. Recaptured fish were at large 1-514 days. Highest return rates were from Horseshoe Reef (34.6%), Naples Reef (23.7%), and the

TABLE 2.—Percentage recapture of tagged olive rockfish at the study sites off Santa Barbara, Calif.

Site	Number tagged	Median time at large (days)	Percentage recovered
Horseshoe Reef	75	309	34.6
Naples Reef	177	156	23.7
Platforms Houchin, Hogan, Hope	513	172	15.2
Talcott Shoals, Santa Rosa Island	159	371	9.4
Fraser Pt., Santa Cruz Island	81	302	7.4
Deephole Reef	369	42	6.5
Rincon Oil Island	17	18	5.8
1 Mile Reef	240	291	5.0
4 Mile Reef	99	112	3.0
Other sites[1]	117	—	0.0
Total	1,847		11.2

[1]Platform Hilda, Platform Holly, Anacapa Island, Smuggler's Cove.

three oil platforms off Summerland (15.2%), all of which were heavily fished by partyboats. Eighty-one percent of all returns were made by partyboat fishermen.

Only the fish tagged around the Summerland oil platforms showed any movements; here nine moved from one platform to another (about 0.8 km).

Regarding biological tags, only the incidence of infection of *Microcotyle sebastis* (Table 3) differed significantly among study sites. Naples Reef and Ellwood Pier differed significantly from the other four sites: a G-test of independence (Sokal and Rohlf 1969) was significant when all six sites were included ($G = 186.45$, $P<0.005$), but not significant when only the oil platforms, 4 Mile Reef, and Horseshoe Reef were included ($G = 1.14$, $0.9>P>0.5$). Naples Reef also differed significantly from Ellwood Pier ($G = 16.8, P<0.005$).

There was no seasonality in incidence of infection, as G-tests of independence among four seasons were not significant for any site (Table 3).

To test whether environmental conditions at Ellwood Pier were suitable for the monogenetic trematodes, tagged fish from Horseshoe Reef infected with *M. sebastis* were introduced into the site. Untagged fish were collected 1 and 6 mo later. After 1 mo 2 of 20 untagged fish (10%) were infected and after 6 mo 7 of 20 (35%) were infected (not a significant difference, $G = 3.6$, $0.1>P>0.05$). The presence of *M. sebastis* in the population seems to indicate that conditions were suitable for the trematode.

Fish lengths averaged significantly shorter ($t = 9.3$, $P<0.001$) at the heavily fished Naples Reef than at the lightly fished Haskels site (Figure 2). Most fish taken from Naples Reef were prereproductive, while mature individuals made up about 45% of the Haskels catch.

DISCUSSION

Kabata (1963) lists five criteria which should ideally be met if a parasite is to be useful as a tag: 1) the parasite should be common in one population and rare or absent in another; 2) the parasite should have a direct life cycle, infecting only one host species during its life; 3) the parasitic infection should be of fairly long duration; 4) the incidence of infection should stay relatively stable; 5) environmental conditions throughout the study site(s) must be within the physiological tolerance of the parasite.

Compared with artificial tags, biological tags have both advantages and disadvantages. Artificial tags may alter the normal behavior of the tagged animal, whereas, in most cases, parasites do not. Moreover, the parasite mix of a population is usually the result of long-term processes, and may be a more accurate indicator of movements than short-term tagging studies. On the other hand, parasite tags will not indicate individual movements. Over the past 20 yr, studies using parasites as tags have delineated nursery grounds (Olson and Pratt 1973), spawning grounds (Margolis 1963; Hare and Burt 1976), and discrete or semidiscrete populations (Sindermann 1961; Kabata 1963).

Results of both artificial and biological tagging indicated that olive rockfish rarely moved between shallow water reefs. A good example of this was the apparent lack of movement between Naples Reef and Ellwood Pier. Though only about 2 km apart, no tagged Naples Reef fish were taken at Ellwood Pier or anyplace else, nor were any of the *M. sebastis* found to be infecting Ellwood Pier fish before I introduced it, though they infect Naples Reef fish.

Like other monogeneans, *M. sebastis* has a direct (one host) life cycle. The maximum distance the infective oncomiricidium larval stage can travel before finding a host is not known, though it is probably limited to a few meters (Llewellyn 1972). Apparently, Ellwood fish were not parasitized because they were sufficiently isolated

TABLE 3.—Incidence of parasite *Microcotyle sebastis* in 80 olive rockfish sampled 20/mo from each of six sites off Santa Barbara, Calif. P values reflect G-tests of independence (Sokal and Rohlf 1969) for incidence of infections among four seasons.

Site	Number infected (1976-77)				Total	P	Percent
	June-Aug.	Sept.-Nov.	Dec.-Feb.	Mar.-May			
Ellwood Pier	0	0	0	0	0	—	0.0
Naples Reef	4	3	3	4	14	$0.9>P>0.5$	17.5
Platform Houchin	12	12	14	15	51	$0.5>P>0.1$	63.8
Platform Hillhouse	10	14	13	15	52	$0.9>P>0.5$	65.0
Horseshoe Reef	14	11	15	15	55	$0.9>P>0.5$	68.8
4 Mile Reef	17	13	15	12	57	$0.9>P>0.5$	71.2

from others to escape exposure to infected fish, even pelagic larvae.

Yet, neither tagging nor parasite data indicated whether fish move offshore from the Ellwood area to Naples Reef. However, size-frequency data of fish taken on Naples Reef and at Haskels (adjacent to the Ellwood Pier) (Figure 2), are evidence that there was probably little movement from Ellwood to Naples. Naples Reef harbors primarily juvenile and preadult olive rockfish (Love and Ebeling 1978) and adults are rarely observed (Ebeling[5]). Apparently, fishing pressure removes fish before they can mature. However, adults were abundant at the lightly fished Ellwood Pier, and limited sampling along a 16 km stretch of kelp inshore of Naples Reef indicated that mature fish were common throughout the bed. Apparently, few of these fish move across the sandy stretch between Naples Reef and the inshore bed.

Though inshore movements seem to be inhibited by stretches of sandy bottom, movement from one oil platform to another obviously is not: tagged fish must traverse at least 0.8 km over sandy bottom with a depth of about 50 m to reach the adjacent site. Miller and Geibel (1973) observed a similar greater mobility in deep waters for blue rockfish, *S. mystinus*.

Olive rockfish off Santa Barbara feed primarily on midwater organisms (nekton and plankton) rather than substrate-oriented prey (Love and Ebeling 1978). It is not known whether these prey are less abundant at the platforms compared with inshore waters. However, if they are less abundant, olive rockfish might be more likely to leave the platform to follow prey. I have noted olive rockfish feeding on anchovies as much as 300 m away from the platforms. Perhaps in these instances some fish may not return to the original platform.

This study emphasized movements of fish that inhabit isolated reefs. Little work was done on fish from the extensive area of continuous kelp forest which grows mostly on sandy bottom and parallels most of the Santa Barbara coast, because sampling is more time consuming in such areas of low rockfish densities. Moreover, much of the tagging was done aboard partyboats which rarely fish these extensive beds. It is quite possible that olive rockfish in kelp beds move about considerably more than those on isolated reefs. I suspect that the limited movements observed may be due to the lack of cover on the relatively barren bottom surrounding the reeflike study sites. Olive rockfish have been rarely taken over sand, either in otter trawls (Ebeling et al.[6]), or seen in underwater transects in kelp beds over a sand bottom (Quast 1968), and seem to be strongly attracted to high-relief substrate, such as that of platforms and rocky reefs. Kelp beds may provide "bridges" from one reef to another.

Previous studies (Table 4) indicate that many other shallow water rockfish exhibit limited movements. The two most extensively investigated benthic species, *S. carnatus* and *S. chrysomelas*, defend small feeding territories and shelter holes (Larson 1977; Hallacher 1977). Also, agonistic displays by *S. serriceps* (Feder et al. 1974; Haaker 1978) and long-term residence in particular crevices by *S. nebulosus* (McElderry[7]) indicate that these benthic species may also be territorial. Thus, it seems likely that most or all benthic reef rockfish may move relatively little.

Similarly, some midwater rockfishes that live over these shallow reefs, seem to stay within a fairly small area. In particular, tagging of *S. mystinus* (Miller and Geibel 1973) indicated restricted movements, and tagging of *S. flavidus* (Carlson and Haight 1972) showed that this species has a strong homing tendency. However, movements of tagged *S. melanops* (Coombs 1979), along with pelagic capture (Dunn and Hitz 1969) indicate that it probably moves about extensively.

Relatively parochial midwater rockfish, such as *S. mystinus, S. serranoides*, and *S. flavidus*, do not appear to be territorial, in the sense that a territory is a "defended" (Noble 1939) or "exclusive" (Schoener 1968) area. Indeed, these species often form single or multispecies aggregations of thousands of individuals, which show little or no agonistic behavior. The sizes of rockfish home ranges have not been estimated, though Miller and Houk[8] believed that *S. mystinus* aggrega-

[5]Ebeling, Alfred W. Department of Biological Sciences, University of California, Santa Barbara, CA 93106, pers. commun. February 1978.

[6]Ebeling, A. W., W. Werner, F. A. Dewitt, Jr., and G. M. Cailliet. 1971. Santa Barbara oil spill: short-term analysis of macroplankton and fish. EPA, Water Qual. Off. Doc. no. 15080EA02/71, 68 p.

[7]H. McElderry Department of Biology, University of Victoria, Victoria, B.C. pers. commun. January 1978.

[8]D. Miller and J. Houk, California Department of Fish and Game, 2201 Garden Road, Monterey, CA 93940, pers. commun. January 1978.

TABLE 4.—Summary of published observations on rockfish, *Sebastes* spp., movements in the northeast Pacific.

Species	Location	Method	Results	Source
S. alutus	Northeast Pacific Ocean	Analysis of fish catch data	Seasonal bathymetric movements of many kilometers and 100 m in depth	Review in Gunderson (1977)
S. atrovirens	Monterey, Calif.	Tagging	No movement	Miller and Geibel (1973)
S. auriculatus	Monterey	Tagging	No movement	Miller and Geibel (1973)
	Humboldt Bay, Calif.	Tagging	No movement	DeWees and Gotshall (1974)
S. carnatus	Santa Barbara Channel, Calif.	Underwater observation, tagging	Has home range; no evidence of extensive movement	Larson (1977)
	Monterey region, Calif.	Underwater observation, tagging	No movement	Hallacher (1977)
S. caurinus	Monterey Bay, Calif.	Tagging, underwater observation	Limited movement, farthest 2.4 km	Miller and Geibel (1973)
	Monterey region	Tagging	No movement	Hallacher (1977)
	Humboldt Bay	Tagging	No movement	Dewees and Gotshall (1974)
	Puget Sound, Wash.	Underwater observation	Fewer individuals seen in shallow water during summer	Dewees and Gotshall (1974) Patten (1973)
	Puget Sound	Underwater observation	Very limited bathymetric and onshore-offshore movement, a few meters vertical movement between summer and winter	Moulton (1977)
S. chrysomelas	Santa Barbara Channel	Underwater observation, tagging	Species has home range, no evidence of extensive movement	Larson (1977)
	Monterey region	Underwater observation, tagging	No movement	Hallacher (1977)
	Monterey Bay	Tagging	No movement	Miller and Geibel (1973)
S. flavidus	Puget Sound	Underwater observation	Very limited bathymetric and onshore-offshore movement, a few meters vertical movement between summer and winter	Moulton (1977)
	Alaska	Tagging	Homing study, species homed up to 22.5 km	Carlson and Haight (1972)
S. melanops	Monterey	Tagging	No movement	Miller and Geibel (1973)
	Humboldt Bay	Tagging	No movement	DeWees and Gotshall (1974)
	Oregon	Tagging	Limited number of recoveries, 2 of the 10 recovered fish moved, one 619 km, other 24 km	Coombs (1979)
	Puget Sound	Underwater observation	Very limited bathymetric and onshore-offshore movement, a few meters vertical movement between summer and winter	Moulton (1977)
	Gulf of Alaska	Capture	Review of pelagic captures	Dunn and Hitz (1969)
S. miniatus (Juv.)	Redondo Beach, Calif.	Tagging	Movement of 8-9.6 km	Turner et al. (1969)
(Juv.?)	Monterey	Tagging	No movement	Miller and Geibel (1973)
S. mystinus	Southern to northern Calif.	Tagging	Generally little or no movement; slight movement in deeper water	Miller and Geibel (1973)
	Monterey Bay	Tagging	Restricted movement	
S. pinniger	Monterey Bay	Tagging	No movement	Miller and Geibel (1973)
S. rosaceus	Monterey region	Underwater observation	No movement	Hallacher (1977)
S. ruberrimus	Oregon	Tagging	No movement	Coombs (1979)
S. serranoides	Santa Monica Bay Calif.	Tagging	No movement	Turner et al. (1969)
	Santa Barbara Channel	Tagging	No movement in shallow water, limited movement in deeper water	Present paper

tions are quite patchy within a kelp bed and some fish may remain within a very limited area for extended periods. In kelp beds, individuals of *S. serranoides* may move about more than those of *S. mystinus*. Miller and Houk noted that *S. serranoides* individuals were not seen as consistently as those of *S. mystinus* in kelp-bed transects in Monterey Bay. As *S. mystinus* preys primarily on plankton and animals on plant surfaces (Gotshall et al. 1965; Hallacher 1977; Love and Ebeling 1978), it seems likely that this species spends much of its time waiting for prey to drift by. *Sebastes serranoides* feeds somewhat more on moving prey (Love and Ebeling 1978) and so may forage more widely.

Some seasonal movement of rockfish may also occur, at least north of Pt. Conception. A number of studies report that rockfish numbers on shallow water reefs seem to decrease during winter (Miller and Geibel 1973; Moulton 1977; Burge and Schultz[9]). Increased turbulence may drive the fish into deeper water or into reef shelters where they are less visible. Ebeling (see footnote 5) observed no winter decrease in rockfish abundance at Naples Reef. The waters of the Santa Barbara Channel are considerably less turbulent

[9]Burge, R. T., and S. A. Schultz. 1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. Calif. Dep. Fish Game, Mar. Res. Tech. Rep. 19, 433 p.

than those above Pt. Conception; perhaps here fish can remain on the reefs despite winter storms. Miller and Geibel (1973) noted a sharp winter decrease in *S. mystinus* numbers on a reef in Monterey Bay. Yet despite extensive tagging at this site and intensive sampling and underwater observation of surrounding reefs during winter, no tagged individuals were found at other reefs (Miller and Houk see footnote 8). Factors other than turbulence may account for a winter exodus. Some rockfish species may leave inshore reefs to spawn. If fish do leave the reef, the extent of their movement is, in general, not known. Moulton (1977) found that during winter rockfish on Puget Sound reefs retreated only short distances, into slightly deeper water.

The between site difference in mean fish length found between Naples Reef and Haskels probably reflects a difference in fishing pressure. The more heavily fished site averaged smaller fish and fewer mature ones because larger fish were selectively angled, or have been subjected to fishing effort for a longer period and are thus more likely to be caught.

As heavily fished sites contain primarily prereproductive individuals (as, in general, does Naples Reef), reproduction of mature fish at lightly fished sites could account for much of the recruitment for all areas.

Based on data from mechanical and parasite tags, olive rockfish off Santa Barbara exhibit very restricted movements on shallow water reefs, but may be somewhat more mobile around deeper water oil platforms. The species' parochialism in shallow water makes it susceptible to overexploitation as interchange of individuals from other reefs is rare.

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TRENDS TOWARD DECREASING SIZE OF BROWN SHRIMP, *PENAEUS AZTECUS*, AND WHITE SHRIMP, *PENAEUS SETIFERUS*, IN REPORTED ANNUAL CATCHES FROM TEXAS AND LOUISIANA[1]

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ABSTRACT

An exponential model adequately characterized the size composition (expressed as a regression of transformed cumulative percentage of weight on size category) of reported annual catches of brown and white shrimp in Texas and Louisiana from 1959 to 1976. Louisiana catches contained considerably greater proportions of small shrimp than did Texas catches. For both species and States, there was a significant trend toward increase in proportion of small shrimp in the catches over the period.

The size composition of a stock has long been used as a simple criterion for assessing the status of a fishery (Henderson 1972; Ricker 1975). Decreasing average size of individuals can be an indication of increasing mortality (usually equated with increased fishing mortality) or decreasing growth (usually attributed to overcrowding). This paper develops a new and simple approach to assessing size composition of catches, and uses it to detect differences and trends in size composition of brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, catches in Texas and Louisiana.

We chose to compare Texas and Louisiana shrimp fisheries because 1) they are regulated by substantially different laws (Christmas and Etzold 1977), resulting in different size distributions of shrimp harvested within the two States, and 2) they are adjacent States which together produced the bulk (75%) of the reported shrimp catch from inshore and offshore waters of the U.S. coast of the Gulf of Mexico in 1975. Inshore refers to estuarine or bay waters landward of barrier islands, and offshore refers to waters seaward of barrier islands.

Texas shrimp laws provide for licenses, limits on number and size of trawls used per boat inshore, limits on trawl mesh size, daily limits on inshore catch, and size limits on food shrimp (not on bait shrimp) during the fall (15 August-15 December) open season inshore and during all open seasons offshore. No size limits are imposed on food shrimp during the spring (15 May-15 July) open season inshore. All offshore areas are closed to shrimping from 1 June to 15 July, and offshore areas within 7 fathoms are closed from 16 December to 1 February. No nighttime shrimping is allowed inshore. These laws lead to a fishing strategy emphasizing the harvest of larger shrimp offshore, with considerable restriction of harvest of smaller shrimp inshore.

Louisiana shrimp laws provide for licenses, limits on number and size of trawls used per boat inshore, limits on trawl mesh size, and size limits during the fall open season (third Monday in August to 21 December), with the exception that size limits are removed for brown shrimp after 15 November. No size limits are imposed during the spring open season (opened not later than 25 May and extending 50 days thereafter unless closure is warranted to protect young white shrimp). Nighttime shrimping with "butterfly nets" (wing nets) is allowed inshore. These laws encourage a fishing strategy emphasizing harvest of considerable quantities of small shrimp inshore as well as harvest of larger shrimp offshore.

Brown and white shrimp spend the juvenile and subadult phases of their life cycles inshore, and the adult and larval phases offshore (Caillouet and Patella 1978), thus recruitment to the fishery begins in the juvenile or subadult phases. The entire life cycle is completed within a year, therefore the shrimp crop in a given year depends upon recruitment in that year. Environmental

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factors affecting maturation and spawning of adults and survival of larvae, juveniles, and subadults apparently have pronounced influences on recruitment. While some maturation and spawning takes place year around, peaks occur in spring and fall.

The size composition of the reported annual catches of brown and white shrimp greatly affects the value of these catches. For the years 1959-75, Caillouet and Patella (1978) estimated that the ex-vessel value (expressed in dollar units based upon 1975) of reported annual catches of brown shrimp in Texas was 1.6 times greater than that in Louisiana, for a given weight of catch. For white shrimp, it was 1.2 times greater in Texas than in Louisiana. They attributed these differences in value of the catches to differences in size composition of the catches because larger shrimp command higher prices than do smaller shrimp on the market. In addition, they were impressed that the size composition of reported catches of brown and white shrimp had remained remarkably constant within each State despite wide variations in weight of the annual catch from year to year in response to fluctuations in recruitment.

DESCRIPTION OF DATA

This paper deals with combined inshore and offshore reported annual catches of brown shrimp and white shrimp from the Texas coast (statistical areas 18-21) and Mississippi River to Texas (statistical areas 13-17), representing the Texas coast and that part of the Louisiana coast west of the Mississippi River, respectively (Figure 1), and from 1959-76 (U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78).

The annual catches reported in the Gulf Coast Shrimp Data (U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78) represent only a portion of the total annual catches; those landed by United States craft at U.S. ports along the coast of the Gulf of Mexico. Portions not reported include some of the commercial landings (including those of foreign fishing craft), undersized shrimp that are discarded, and landings by domestic sport fishermen. The proportion of the total annual catch that is not reported is unknown, and we do not know what effect its inclusion would have on size composition of the annual catch. However, we believe that the reported catch represents the bulk of the total catch and that the reported catch is a reasonably good reflection of the combined effects of shrimp population characteristics (growth and natural mortality) and removals by fishing (or fishing mortality).

Size composition of the reported catches was examined in units of pounds (as reported in catch statistics) caught in eight "count" or size categories representing number of shrimp per pound, heads-off ($\geq$68, 51-67, 41-50, 31-40, 26-30, 21-25, 15-20, and $<$15). These categories are approximately equivalent to the following number of shrimp per kilogram (heads-off), respectively: $\geq$150, 112-148, 90-110, 68-88, 57-66, 46-55, 33-44, and $<$33. The use of count (number per pound) as a measure of shrimp size amounts to a reciprocal transformation of the weight (W) per shrimp (in pound):

$$\text{Count} = \frac{1}{W}$$

The same would be true if count and weight per shrimp were expressed in metric units. Kutkuhn (1962) described biases associated with determination of size composition of reported shrimp catches, including those resulting from interview sampling methods, from prevailing practices of catch culling, grading or sorting, and from catch sampling practices. Because the methods used to determine size composition of catches have remained essentially unchanged from 1959 to 1976 (Farley[3]), we believe that the biases would have

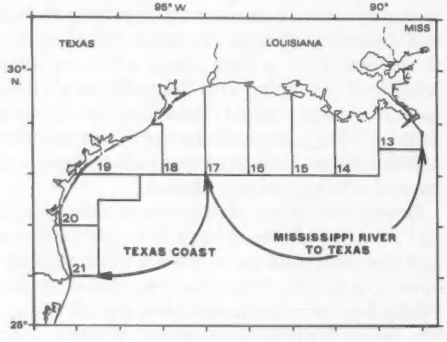

FIGURE 1.—Statistical areas used in reporting Gulf Coast Shrimp Data for Mississippi River to Texas and Texas coast.

[3]Orman Farley, National Marine Fisheries Service, NOAA, Galveston, Tex., pers. commun. December 1978.

more or less constant effects on comparisons between Texas and Louisiana and over the period from 1959 to 1976, and therefore would have only minor if any effects upon our conclusions. We further recognize that each size category may include representatives of more than one peak of recruitment, since they include catches taken over the period of 1 calendar year. Therefore, it is likely that any differences or trends in the time phasing of peak fishing activity within Texas and Louisiana within a year could contribute to the observed differences and trends in size composition of the respective catches in the two States.

ANALYTICAL METHODS

Percentage (by weight, heads-off) was determined for each size category in reported annual catches of brown and white shrimp from Texas coast and Mississippi River to Texas for each of the years from 1959 through 1976 (see Caillouet and Patella 1978). Cumulative percentage (F) for each size category was then determined for catches of both species, from Texas coast and Mississippi River to Texas, and for each year. Percentages were summed from the smallest shrimp (highest count, ⩾68) to the largest (lowest count, <15).

An exponential model was chosen to represent the relationship between cumulative percentage, F, and size category, C, for brown and white shrimp, for Texas coast and Mississippi River to Texas, and for the years 1959-76 as follows:

$$\hat{F}_i = ae^{bC_i}$$

where F_i = cumulative percentage (by weight, heads-off) of catch in ith size category
C_i = lower limit of ith size category ($C_1 = 15, C_2 = 21, \ldots, C_7 = 68$)
i = $1, 2, \ldots, 7$
a = constant
b = exponent
e = base of natural logarithm.

The cumulative percentages, F, were transformed to natural logarithms, and the logarithmic form of the model was used to estimate parameters by least squares:

$$\ln F_i = \ln(a) + bC_i = \epsilon$$

where ϵ = residual (deviation from regression).

Thus, the logarithmic form of the model describes the relationship between transformed cumulative percentage and size category, and represents size composition of the reported annual catches. Note that this linear relationship describing size composition of the reported annual catches is achieved by transforming both the cumulative percentage to ln F and the weight per shrimp (in pound, heads-off) to count (number per pound).

Midpoints of size categories were not used because the size categories have unequal intervals, an unavoidable result of using data based on size categories developed by the shrimping industry. Upper limits of size categories were not used, because we could not determine the upper limit of the ⩾68 category, and this category represented a significant proportion of the catches. Also, we did not use the <15 size category because we could not determine its lower limit (zero was not realistic), and this category represented a very small fraction of the catches. Apparently, total mortality (natural and fishing combined) is such that relatively small portions of the shrimp populations survive to be caught at sizes as large as <15/pound. Because lower limits of size categories were used for regression analyses, and because the <15 size category was not used in the analysis, the magnitude of the ordinate intercept, ln(a), is of no particular use. It is the slope, b (= exponent of the exponential model) that is of most interest and use as an index showing the rate of change in ln$F$ with C. Extrapolation below 15 count is not advised, because the linear relationship does not apply beyond this point.

In order to determine whether size composition of the reported annual catches changed with time, the slopes, b, of the regressions of transformed cumulative percentage on size category were plotted against years, and straight lines were fitted to points b and x (= last two digits of each year) by least squares, for brown and white shrimp from the Texas coast and Mississippi River to Texas, 1959-76 (Figures 2, 3).

RESULTS AND DISCUSSION

Slopes, b, of the regressions of transformed cumulative percentage versus size category, all differed significantly from zero at the 99.9% level of confidence, showing that the linear fit was good (Tables 1, 2). The slopes changed with time as

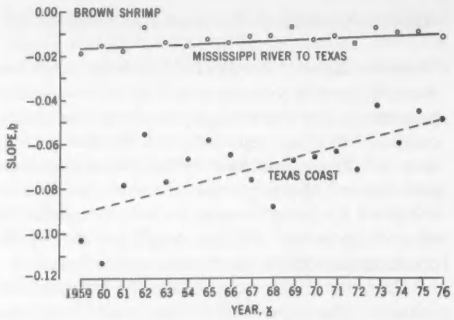

FIGURE 2.—Trends in slope (b) of regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown shrimp in Mississippi River to Texas (solid line, circles) and Texas coast (dashed line, dots) 1959-76 (data from Tables 1, 2).

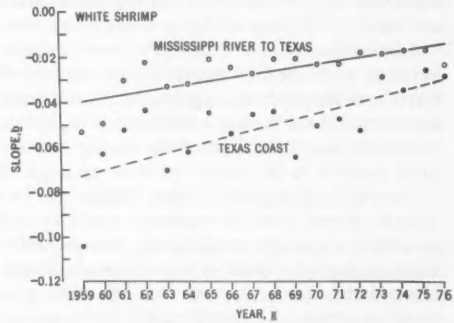

FIGURE 3.—Trends in slope (b) of regressions of transformed cumulative percentage ($\ln F$) on size category (C) for white shrimp in Mississippi River to Texas (solid line, circles) and Texas coast (dashed line, dots), 1959-76 (data from Tables 1, 2).

shown by positive trends that were significantly different from zero at the 95% level of confidence (Table 3; Figures 2, 3). This change in b with time indicated that the size composition of the reported annual catches of brown and white shrimp shifted during 1959-76 toward greater proportions of shrimp of smaller size in the catches. This shift was more pronounced in Texas, but the Louisiana catches contained considerably greater proportions of small shrimp than did those of Texas. Points for 1959 and 1960 may be less reliable than those for later years because the Gulf Coast Shrimp Data reports were released for the first time in 1956, and by 1961 the data collection methods had been greatly refined. Elimination of data points for 1959 and 1960 decreased all the

TABLE 1.—Linear regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown and white shrimp, Mississippi River to Texas (based on U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78).[1]

	Brown shrimp			White shrimp		
Year	ln(a)	b	r^2	ln(a)	b	r^2
1959	4.881	−0.0196	0.962	5.508	−0.0537	0.992
1960	4.767	−0.0154	0.978	5.468	−0.0496	0.988
1961	4.842	−0.0180	0.976	5.097	−0.0301	0.990
1962	4.696	−0.0077	0.994	5.005	−0.0222	0.968
1963	4.823	−0.0144	0.980	5.273	−0.0336	0.960
1964	4.817	−0.0156	0.927	5.101	−0.0318	0.998
1965	4.749	−0.0126	0.992	4.849	−0.0206	0.996
1966	4.795	−0.0144	0.988	5.003	−0.0248	0.952
1967	4.786	−0.0119	0.992	4.928	−0.0273	0.994
1968	4.730	−0.0117	0.982	4.849	−0.0207	0.986
1969	4.654	−0.0079	0.947	4.922	−0.0207	0.998
1970	4.747	−0.0135	0.988	4.884	−0.0227	0.986
1971	4.746	−0.0118	0.994	4.936	−0.0230	0.996
1972	4.795	−0.0152	0.992	4.818	−0.0179	0.992
1973	4.601	−0.0080	0.872	4.852	−0.0184	0.996
1974	4.657	−0.0101	0.910	4.767	−0.0171	0.980
1975	4.657	−0.0105	0.910	4.760	−0.0165	0.968
1976	4.712	−0.0112	0.964	4.889	−0.0232	0.980

[1]F = Cumulative percentage of weight caught in each of seven size categories; C = lower limit of each of seven size categories; all b's were significantly different from zero at the 99.9% level of confidence; r^2 = coefficient of determination.

TABLE 2.—Linear regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown and white shrimp, Texas coast (based on U.S. Fish and Wildlife Service 1960-69; National Marine Fisheries Service 1970-78.).[1]

	Brown shrimp			White shrimp		
Year	ln(a)	b	r^2	ln(a)	b	r^2
1959	6.851	−0.1039	0.965	6.848	−0.1042	0.895
1960	6.961	−0.1140	0.957	6.008	−0.0635	0.899
1961	6.069	−0.0790	0.972	5.448	−0.0521	0.990
1962	5.525	−0.0558	0.977	5.369	−0.0436	0.993
1963	5.936	−0.0771	0.988	5.875	−0.0704	0.990
1964	5.743	−0.0669	0.995	5.697	−0.0625	0.994
1965	5.626	−0.0588	0.991	5.268	−0.0449	0.998
1966	5.892	−0.0655	0.984	5.478	−0.0541	0.995
1967	6.016	−0.0764	0.980	5.171	−0.0455	0.991
1968	6.420	−0.0883	0.964	5.462	−0.0440	0.946
1969	5.901	−0.0680	0.969	5.806	−0.0643	0.983
1970	5.737	−0.0661	0.986	5.412	−0.0502	0.994
1971	5.784	−0.0629	0.973	5.302	−0.0476	0.998
1972	6.010	−0.0722	0.979	5.470	−0.0522	0.992
1973	5.427	−0.0437	0.978	5.140	−0.0283	0.976
1974	5.690	−0.0603	0.989	5.023	−0.0343	0.984
1975	5.432	−0.0460	0.991	4.995	−0.0259	0.992
1976	5.457	−0.0478	0.990	5.032	−0.0278	0.995

[1]F = Cumulative percentage of weight caught in each of seven size categories; C = lower limit of each of seven size categories; all b's were significantly different from zero at the 99.9% level of confidence; r^2 = coefficient of determination.

trends in b, and the trend for brown shrimp from Mississippi River to Texas was no longer different from zero at the 95% level of confidence (Table 3). However, elimination of points for the first 2 yr from the trends also reduced the degrees of freedom from 16 to 14 for the test of significance of trends, so the test was less sensitive in this case. Whether or not the apparent trend was real for brown shrimp from Mississippi River to Texas could be determined by examination of data for years beyond 1976, as they become available.

TABLE 3.—Trends in slopes (b) of regressions of transformed cumulative percentage ($\ln F$) on size category (C) for brown and white shrimp, Mississippi River to Texas and Texas coast, 1959-76 vs. 1961-76 (based on data from Tables 1, 2; Figures 2, 3).

	Brown shrimp				White shrimp			
	Mississippi R.-Texas		Texas coast		Mississippi R.-Texas		Texas coast	
Item	1959-1976	1961-1976	1959-1976	1961-1976	1959-1976	1961-1976	1959-1976	1961-1976
Trend[1]	0.00036*	0.00026	0.00244*	0.00141	0.00148*	0.00077*	0.00255*	0.00183*
Trend coefficient of determination	0.332	0.172	0.492	0.289	0.574	0.496	0.542	0.448

[1]Equals slope of the regression of b on x where x is the last two digits of each year.
*The change in slope (b) per year was significantly different from zero at the 95% level of confidence.

There was a positive correlation ($r = 0.702$) between the slopes of regressions of transformed cumulative percentage on size category for brown and white shrimp from Mississippi River to Texas in 1959-76, that was significantly different from zero at the 99% level of confidence. The same was true ($r = 0.742$) for brown and white shrimp from the Texas coast. This indicated that the direction of the shift in size composition of reported catches within a given year was usually in the same direction for both species in a given State (Tables 1, 2).

For a given weight of reported annual catch, the ex-vessel value of shrimp harvested in Louisiana is considerably less than that in Texas (Caillouet and Patella 1978), and this is largely a function of the size composition of the respective catches in the two States. Our analysis cannot distinguish whether the observed differences and trends in size composition of the reported catches are due to differences and trends in fishing mortality, natural mortality, or growth, but we suggest that the predominant causes of the observed differences and trends are differences and trends in fishing mortality. There is no evidence to indicate that separate shrimp stocks exist in these two States, or that natural mortality or growth differ between the two States (see Christmas and Etzold 1977). On the other hand the number and size of shrimp fishing craft and other indices of fishing effort are different in the two States and have increased over time (Christmas and Etzold 1977; Caillouet and Patella 1978). Also, differences and trends in time phasing of peak fishing activity in Texas and Louisiana within a year could have contributed to the differences and trends in size composition reported herein. Regardless of the cause or causes, continued shifts in size composition toward greater proportions of smaller shrimp in the catches can be expected to weaken the ex-vessel value of the catches.

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NOTES

STAGE I ZOEAE OF A CRANGONID SHRIMP, *CRANGON FRANCISCORUM ANGUSTIMANA*, HATCHED FROM OVIGEROUS FEMALES COLLECTED IN KACHEMAK BAY, ALASKA

Information on the larval stages of crangonid shrimp of the North Pacific Ocean is meager. Needler (1941) described the first zoeal stage of *Crangon septemspinosa* (as *Crago septemspinosus* Say) hatched in the laboratory from ovigerous females and the remaining four zoeal stages from plankton collected near Prince Edward Island, Canada. Kurata (1964) described the larval stages of *C. affinis* de Haan and various larval stages of six unidentified *Crangon* spp. from Japanese waters. He obtained the first zoeal stage of *C. affinis* from known parentage, but the remaining stages were collected from plankton. Makarov (1967) briefly described larvae of *C. dalli* Rathbun and *C. septemspinosa* (Say) which were collected from plankton along the western Kamchatka shelf. He suggested that *C. dalli* was an analog of *C. allmani* Kinahan and *C. septemspinosa* was an analog of *C. crangon* (Linnaeus). *Crangon allmani* and *C. crangon* are eastern Atlantic species. He assumed that the *C. affinis* larvae described by Kurata (1964) were actually larvae of *C. septemspinosa*. Loveland (1968) described larvae of *C. alaskensis* Rathbun reared in the laboratory from females collected near Anacortes, Wash.

Morphology of Stage I larvae is closely related to Caridean development and can be used to estimate the number of larval stages, classify species, categorize larvae for identification purposes, and identify subsequent larval stages (Needler 1938; Pike and Williamson 1961, 1964; Kurata 1964; Ivanov 1971; and others). In this report I describe and illustrate the first zoeal stage of *C. franciscorum angustimana* Rathbun from ovigerous females and compare these zoeae with Stage I zoeae of crangonids described by other authors. Also, I show that the criterion of the absence of exopodites on the second pair of pereopods for distinguishing larvae of *Crangon* from other genera of the Crangonidae is invalid for Crangonidae of the North Pacific Ocean.

Methods

Ovigerous *C. franciscorum angustimana* were caught at 30 m (16 fathoms) in shrimp pots in early May 1976 in Kachemak Bay, Alaska. Four females were kept in seawater in a plastic bucket for about ½ h and then each female was put into a 4 l glass jar containing filtered, aerated seawater. The water was about 35‰ salinity, about 6°C, and was changed daily until zoeae were released, about 5 days later. Most zoeae were released at night. I did not determine whether the larvae were hatched as prezoeae.

Terms used in the text, nomenclature of gills and appendages, and techniques of measurement and illustration are given by Haynes (1976). As an aid to the study of segmentation and setation, some larvae were cleared in 10% KOH and the exoskeleton stained with Turtox[1] CMC-S (acid fuchsin stain mountant). Only the left number is figured because the paired appendages of the larvae are symmetrical; except, the mandibles are drawn as a pair. There was no morphological variation, except variation in total length, among the zoeae used for the description.

Stage I Zoea

Mean total length of Stage I zoeae (Figure 1A) was 3.1 mm (range 2.8-3.3 mm; 10 specimens). Rostrum slender, spiniform, without teeth, about one-third length of carapace. Carapace with small rounded prominence near posterior margin. Two distinct denticles immediately posterior to pterygostomian spine; no supraorbital or antennal spines. Eyes sessile.

ANTENNULE (Figure 1B).—First antenna, or antennule, an unsegmented peduncle (inner flagellum) bearing a conical projection and a setulose spine. Conical projection bears a simple seta and three aesthetascs of about equal length.

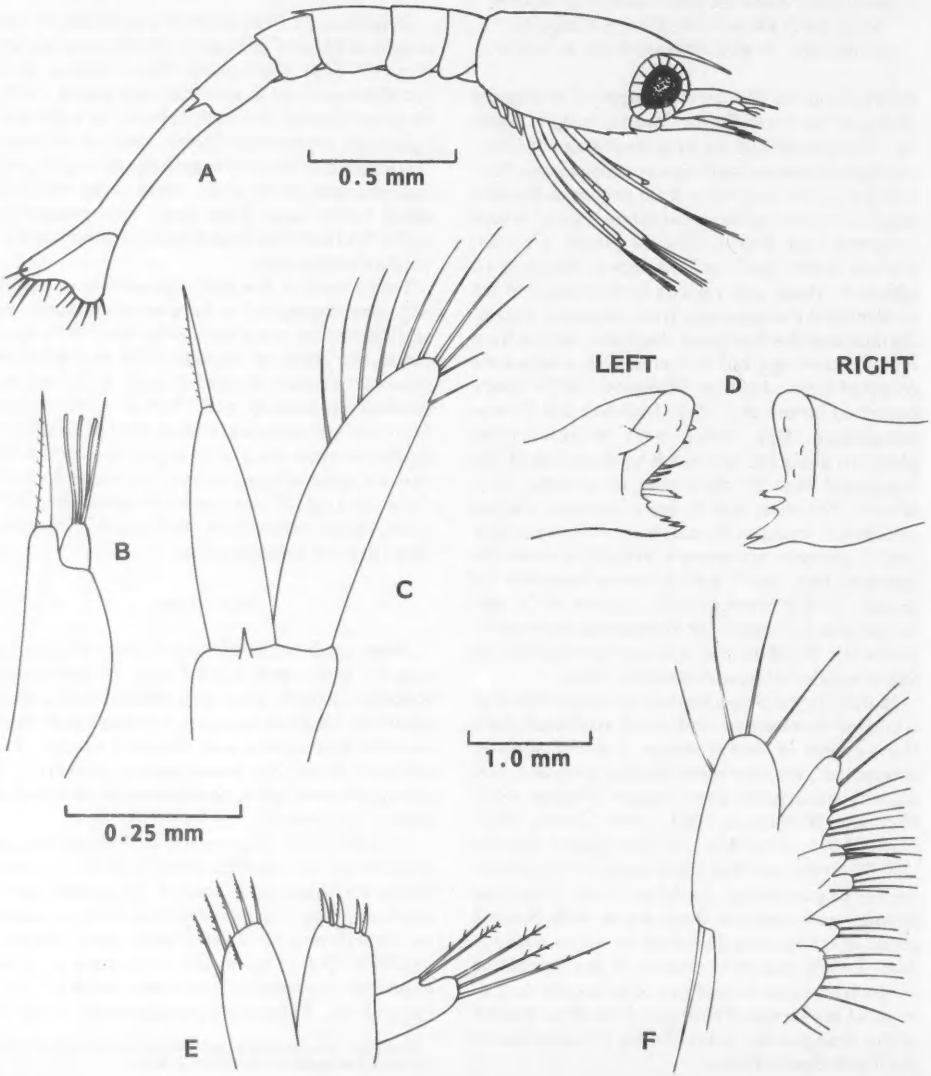
ANTENNA (Figure 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum unsegmented, slightly

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

shorter than scale, bears a setulose spine. Antennal scale not distally segmented, fringed with nine heavily plumose setae and subterminal plumose seta on outer margin. Protopodite bears spine at base of flagellum but not at base of scale.

MANDIBLES (Figure 1D).—Without palps; well developed. Incisor process of left mandible bears three teeth in contrast to biserrate incisor process of right mandible. Left mandible bears a movable premolar denticle (lacinia mobilis) adjacent to incisor process and large subterminal tooth on truncated molar process.

MAXILLULE (Figure 1E).—First maxilla, or maxillule, bears coxal and basial endites and an



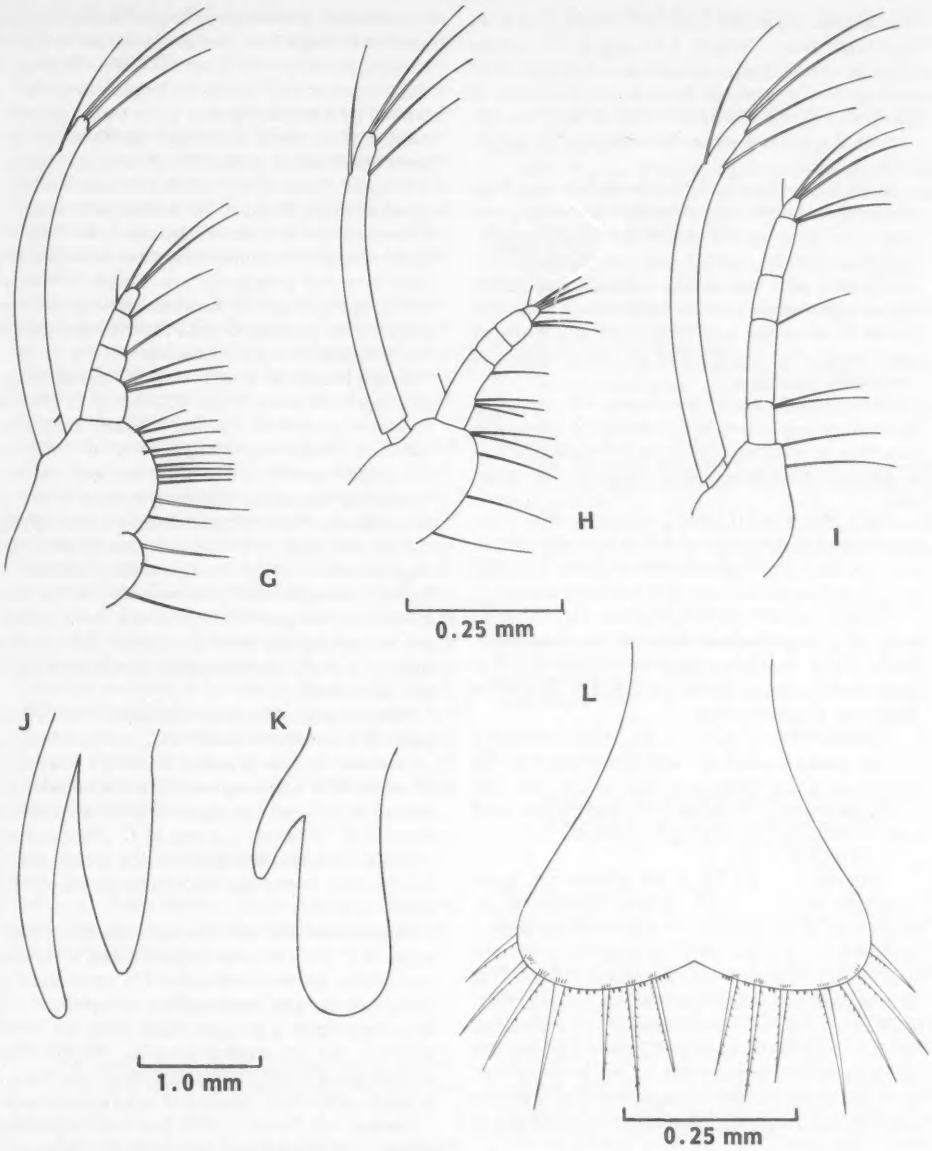


FIGURE 1. — Stage I zoeae of *Crangon franciscorum angustimana:* A, whole animal, right side; B, antennule, ventral; C, antenna, ventral; D, mandibles, left and right, posterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, dorsal; H, second maxilliped, dorsal; I, third maxilliped, dorsal; J, first pereopod, right side; K, second pereopod, right side; L, telson, dorsal. Setules on setae are omitted for clarity; spinulose setae are shown.

endopodite. Proximal lobe (coxopodite) bears six spinulose setae. Median lobe (basipodite) bears five spinulose spines terminally. Unsegmented endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal spinulose setae. No outer seta on maxillule.

MAXILLA (Figure 1F).—Exopodite (scaphognathite) bears four long plumose setae and a proximal seta; proximal end not projected posteriorly. Endopodite unsegmented; bears eight setae. Both basipodite and coxopodite bilobed. Basipodite bears eight setae, four on each lobe. Coxopodite bears 10 setae, three on distal lobe and seven on proximal lobe. Most setae on basipodite and coxopodite spinulose.

FIRST MAXILLIPED (Figure 1G).—Unsegmented protopodite bilobed; bears 14 setae. Endopodite four-segmented; setation formula 4, 1, 1, 3. Exopodite bears four natatory setae. No epipodite.

SECOND MAXILLIPED (Figure 1H).—Unsegmented protopodite not lobed; bears five setae. Endopodite four-segmented; setation formula 5, 2, 0, 5. Exopodite bears five natatory setae.

THIRD MAXILLIPED (Figure 1I).—Unsegmented protopodite not lobed; bears two setae. Endopodite nearly as long as exopodite; five-segmented; setation formula 4, 2, 0, 1, 2. Exopodite bears five natatory setae.

PEREOPODS (Figure 1J, K).—Only pairs one to four present; pairs one and two (Figure 1J, K) biramous, pairs three and four uniramous. All pereopods poorly developed, unsegmented, and compacted tightly under cephalothorax.

PLEOPODS.—Absent.

ABDOMEN AND TELSON (Figure 1A, L).—Abdomen consists of five somites (somite six is fused with telson in Stage I). Third somite bears a dorsal spine on posterior margin; fifth somite bears pair of spines on posterolateral margin that extend posteriorly about one-fourth length of fifth abdominal somite. Telson emarginated distally; bears 7 + 7 pairs of densely plumose setae. Minute spinules at base of each seta, except possibly last pair, and along posterior margin of telson to fourth setal pair and on setae themselves. No anal spine.

Comparisons of Zoeal Stage I With Descriptions by Other Authors

Of the published descriptions of Stage I zoeae of *Crangon* spp. from the North Pacific Ocean, Stage I zoeae of *C. franciscorum angustimana* are most similar to Stage I zoeae of *C. alaskensis*, *C. affinis*, *C. septemspinosa*, and Kurata's (1964) "Species A" and "Species D." These examples are characterized by a median dorsal spine on the posterior margin of the third abdominal somite and by posterolateral spines on the fifth abdominal somite.

Stage I zoeae of *C. alaskensis* can be distinguished from Stage I *C. franciscorum angustimana* by the rostrum and pereopods. In Stage I *C. alaskensis* the rostrum does not extend beyond the eyes and the pereopods are absent (Loveland 1968), but in Stage I *C. franciscorum angustimana* the rostrum extends beyond the eyes and the larvae bear undeveloped pereopods 1-4.

Stage I zoeae of *C. affinis* and "Species A" are distinguished from Stage I zoeae of *C. franciscorum angustimana* by the presence in Stage I zoeae of *C. affinis* and "Species A" of a shallow transverse groove in the carapace and two subterminal setae along the outer margin of the antennal scale. Also in Stage I *C. affinis* and "Species A," the endopodite of the third maxilliped is four segmented. In Stage I zoeae of *C. franciscorum angustimana*, the carapace does not have a shallow transverse groove; there is only one subterminal seta along the outer margin of the antennal scale; and the endopodite of the third maxilliped is five segmented.

Stage I zoeae of Kurata's "Species D" are distinguished from Stage I zoeae of *C. franciscorum angustimana* by the presence in Stage I zoeae of "Species D" of a five-segmented endopodite on the second maxilliped and pleopods that occur as distinct buds. In Stage I zoeae of *C. franciscorum angustimana*, the endopodite of the second maxilliped is four segmented and there are no pleopod buds.

Stage I zoeae of *C. septemspinosa* are like Stage I zoeae of *C. franciscorum angustimana* with some exceptions: the antennal scale of *C. septemspinosa* bears five plumose setae and the endopodite of the first maxilliped is unsegmented (Needler 1941); whereas, the antennal scale of *C. franciscorum angustimana* bears 10 plumose setae and the endopodite of the first maxilliped is four segmented.

Tesmer and Broad (1964) described nine zoeal stages of *C. septemspinosa* reared in the laboratory from ovigerous females obtained off Beaufort, N.C. They found distinct morphological differences between their zoeae and zoeae of the same species as described by Needler, especially in the later stages. Based on Tesmer and Broad's descrip-

tion, Stage I zoeae of *C. septemspinosa* can be distinguished from Stage I zoeae of *C. franciscorum angustimana* by the exopodites of the maxillipeds. The exopodites of the maxillipeds are jointed in Stage I zoeae of *C. septemspinosa* and are not jointed in Stage I zoeae of *C. franciscorum angustimana*. Also, the fifth pair of telson spines are distinctly shorter than the fourth or sixth pair in *C. septemspinosa*; whereas, in my Stage I zoeae of *C. franciscorum angustimana*, the fifth pair of telson spines are about equal in length to the fourth and sixth pairs.

The occurrence in later zoeal stages of functional exopodites on the first pair of pereopods but not on pereopodal pairs 2-5 has been used as a criterion for distinguishing larvae of the genus *Crangon* from larvae of other genera of the family Crangonidae (Williamson 1960).

I found buds of exopodites on both the first and second pair of pereopods in Stage I zoeae of *C. franciscorum angustimana*. Assuming zoeae of *C. franciscorum angustimana* undergo typical development for crangonid larvae, these buds will become functional exopodites at Stage III or IV (Needler 1941; Kurata 1964; Makarov 1967). The criterion of the absence of exopodites on the second pair of pereopods for distinguishing larvae of *Crangon* from other genera of the Crangonidae, therefore, is invalid for the North Pacific Ocean. Unfortunately, larvae are described for only a few species of crangonids from the North Pacific Ocean, including the genus *Crangon*, and confirmation of the generic characteristics of the larvae is needed.

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LENGTH-WEIGHT RELATIONSHIPS OF WESTERN ATLANTIC BLUEFIN TUNA, *THUNNUS THYNNUS*[1]

The Atlantic bluefin tuna, *Thunnus thynnus*, is seasonally distributed over most of the North Atlantic Ocean from Newfoundland to Brazil and from Norway to the Canary Islands (Gibbs and Collette 1967). There has been a great reduction in the Atlantic-wide catch (including Mediterranean) from 38,500 metric tons (t) in 1964 to 12,500 t in 1973 (Miyake et al. 1974). Because of this, a number of studies have been made and are being continued in order to understand the reason for this decline (Parks 1977; Shingu and Hisada 1977).

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Length-weight, length-to-length, and weight-to-weight relationships are necessary in population analyses for converting one measurement to another. In this paper I present the relationships of the following: round weight-straight fork length, round weight-dressed weight, and straight fork length-curved fork length.

During my review of bluefin tuna literature, I found a lack of information on size relationships. Mather and Schuck (1960) used a length-weight curve based on 778 bluefin tuna from Cape Cod to estimate length. They did not indicate, however, when these fish were collected. They did not give a regression formula for the length-weight relationship, but they did present a straight length-curved length relationship based on 185 measurements fitted by inspection. Rodriguez-Roda (1964, 1971) collected 793 bluefin tuna and then determined the length-weight relationship. Of these, 467 bluefin tuna (prespawning) were entering the Mediterranean during May and June and 326 bluefin tuna (postspawning) were leaving the Mediterranean during July and August 1956, 1958, 1959, and 1961. Butler (1971) determined the length-weight relationship by the standard least squares regression method for 237 giant bluefin tuna caught during July through September 1966 from Conception Bay, Newfoundland. Mather et al. (1974) presented regression equations for converting from weight to length for bluefin tuna from Newfoundland, Libya, and the Bahamas from data supplied by the Fisheries Research Board of Canada, the International Council for the Exploration of the Sea, and the Woods Hole Oceanographic Institution. They also presented an equation for converting dressed weight to round weight. The method of determining the equations, the sample sizes, and time period sampled were not presented. Coan (1976) gave a length, weight, and age conversion table for bluefin tuna of both sexes. He converted length to weight based on a length-weight regression given in Sakagawa and Coan (1974), who had in turn, obtained this regression from Frank J. Mather, Woods Hole Oceanographic Institution. Unfortunately, there was no mention of sample size, location, or date.

Methods

Bluefin tuna length and weight measurements were collected during 1974 through 1977 from various landing points and processing plants along the east coast of the United States from Florida to Maine and from the Bahamas. These fish had been caught by purse seine, rod and reel, handline, and harpoon. Straight fork length (centimeters) was measured by caliper, and curved fork length (centimeters) was measured along the body contour by tape. Round weight (total weight of fish when caught) and dressed weight (head, viscera, and tail removed) were recorded in pounds and later converted to kilograms.

Ricker (1973) showed that the geometric mean (GM) regression can be used for a majority of biological situations as a reasonable and consistent estimate of the functional slope because most of the variability is natural.

The functional (GM) regression was calculated for the logarithmic transformation of the length-weight relationship for 3,578 bluefin tuna taken from May through October. The GM regression was also calculated for the relationship between round weight and dressed weight for 685 bluefin tuna taken from July through September, and for the straight fork length to curved fork length relationship for 606 bluefin tuna taken from July through October.

The general equation for the GM regression as given by Ricker is: $Y = u + vX$, with variables X and Y, and u is the y-axis intercept, where $u = \bar{Y} - v\bar{X}$, v is the slope, and $v = [\Sigma y^2/\Sigma x^2]^{1/2}$, where $y_i = Y_i - \bar{Y}$ and $x_i = X_i - \bar{X}$. The limits on all Σ are $i = 1, \ldots, n$.

The standard error of the slope was computed for each regression equation using the following equation from Ricker (1973): $S_v = [S_{yx}^2/\Sigma x^2]^{1/2}$, where S_v is the standard error of the slope and S_{yx}^2 is the mean square or variance of the observations from the regression line in the vertical direction.

Results and Discussion

Based on the classification system of Rivas and Mather (in press), the fish sampled mainly consisted of two size categories, giant bluefin tuna (>180 cm straight fork length and 130 kg round weight) and small bluefin tuna (<130 cm straight fork length or <45 kg round weight). Based on previous growth studies by Mather and Schuck (1960), the giant fish are probably age 9 and older and the small bluefin tuna are most likely age 4 or younger. Very few medium bluefin tuna (130-180 cm straight fork length and 45-130 kg round weight) probably ages 5 through 8 were sampled.

The functional (GM) regressions for straight fork length-round weight (log transformation), round weight-dressed weight, and straight fork length-curved fork length are presented in Table 1. All of these relationships were characterized by high correlation coefficients. The data points are plotted with regression lines in Figures 1-3. The data points show that the GM regression model fits the data reasonably well for the size ranges studied. Extrapolation beyond the size range of observations may yield erroneous predictions. Regression statistics for each relationship are presented in Table 2.

The use of logarithmic transformations may lead to bias in data estimates (Pienaar and Thomson 1969; Beauchamp and Olson 1973; Lenarz 1974). However, since the mean square error for the round weight-straight fork length logarithmic transformation is low (Table 2), the bias in the data estimate was found to be minimal (1%).

Previous publications have not included standard errors or confidence limits or statistics necessary for their estimation. Therefore, comparisons with my data could not be made. To compare results from my study with studies by other authors, I compared estimates of Y using both their regression equations and mine. Whenever possible, I selected X values at each end of their range of values that corresponded with my range of values. I also compared estimates of Y for an X value taken at the middle of their size range.

TABLE 1.—Functional (GM) regression equation and correlation coefficient for the relationships between round weight (Y) and straight fork length (X), round weight (Y) and dressed weight (X), and straight fork length (Y) and curved fork length (X) for western Atlantic bluefin tuna. Weights in kilograms and lengths in centimeters.

Geometric mean regression equation	r
$\log_{10}$ round weight – $\log_{10}$ straight fork length:	
$\log_{10} Y = -4.52307 + 2.91920 \log_{10} X$	0.997
Round weight – dressed weight:	
$Y = -7.92240 + 1.29607 X$	0.935
Straight fork length – curved fork length:	
$Y = -2.06971 + 0.963300 X$	0.892

My estimates of round weight from straight fork length using the functional (GM) regression agreed most closely with my estimates obtained using the regression equation of Sakagawa and Coan (1974), with the greatest difference in estimates of only 2% occurring for a 270 cm fork length (FL) bluefin tuna. My calculated functional regression estimates next most closely agreed with estimates obtained using the length-weight relationship of Butler (1971), with the largest difference of 6% occurring at 250 cm FL. My esti-

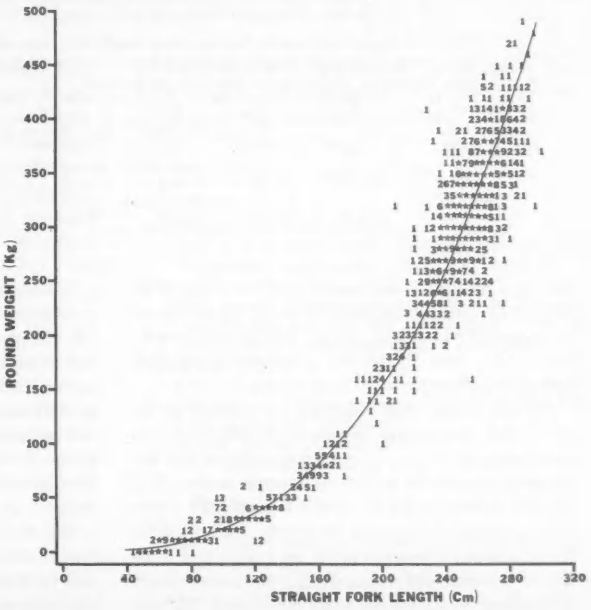

FIGURE 1.—Functional (GM) regression of round weight on straight fork length for 3,578 western Atlantic bluefin tuna 1974-77. (Number of fish indicated, star signifies number >9.)

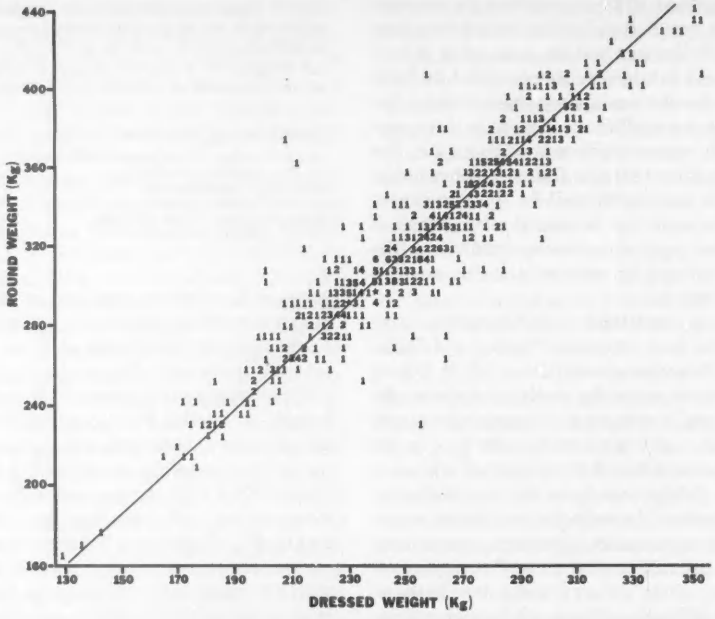

FIGURE 2.—Functional (GM) regression of round weight on dressed weight for 685 western Atlantic bluefin tuna 1974-77. (Number of fish indicated, star signifies number >9.)

TABLE 2.—Regression statistics for $\log_{10}$ round weight (Y) – $\log_{10}$ straight fork length (X), round weight (Y) – dressed weight (X), and straight fork length (Y) – curved fork length (X) of western Atlantic bluefin tuna. Weights in kilograms and lengths in centimeters.

n	$\bar{X}$	$\bar{Y}$	$\sum x^2$	$\sum y^2$	$\sum xy$	S_{yx^2}	S_v
			$\log_{10}$ round weight – $\log_{10}$ straight fork length				
3,578	2.19254	1.87739	222.745	1,896.17	648.054	0.00356051	0.00399809
			Round weight – dressed weight				
685	256.993	325.158	832,635	1,398,650	1,009,090	257.261	0.0175776
			Straight fork length – curved fork length				
606	271.477	259.444	120,979	112,262	103,959	37.9615	0.0177140

mates of weight from length differed most from estimates which I calculated using equations of Rodriguez-Roda (1964, 1971). The largest variation (12%) was found for a prespawning fish measuring 48 cm.

No size range was reported by Mather et al. (1974) for estimating length from weight. However, estimated length corresponding to the extremes and middle of the size range in weight I studied agree closely to values I calculated using their regression equation for Newfoundland, with the greatest difference being only 3% for a 5 kg fish. A greater difference (13%) was noted when comparing estimates from my functional (GM) regression with estimates obtained using their regression equation for the Bahamas for a 5 kg fish. This large difference may have resulted from their not including fish in this size range when calculating their equation because differences at the middle and upper end of my size range were small, 4% or less. There appears to be a typographical error in the equation these authors gave for bluefin tuna from Libya, so no comparison was made.

My functional (GM) regression estimates of round weight from dressed weight agree well with the estimates I obtained using the regression equation of Mather et al. (1974). The largest dif-

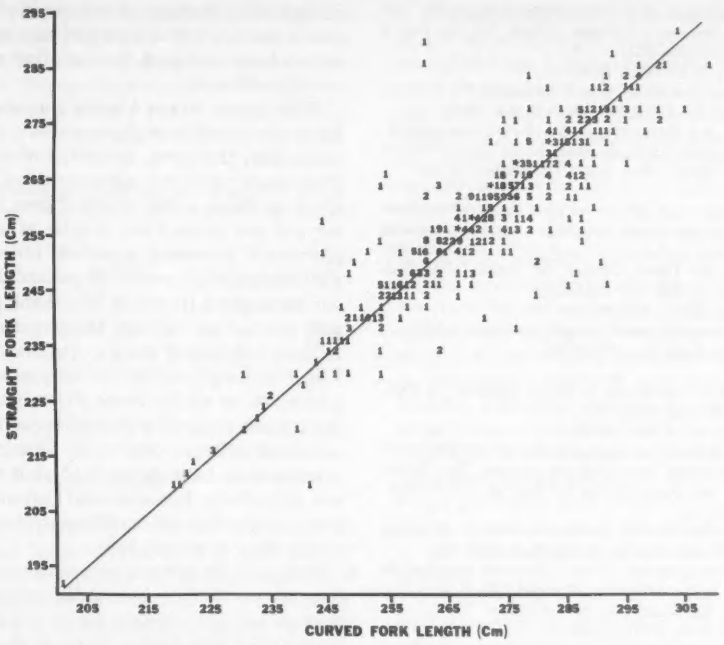

FIGURE 3.—Functional (GM) regression of straight fork length on curved fork length for 606 western Atlantic bluefin tuna 1974-77. (Number of fish indicated, star signifies number >9.)

ference I found was 3% for a 130 cm bluefin tuna. Again I used my range of values for dressed weight since the range was not given by these authors.

My functional (GM) regression estimates of straight fork length from curved fork length agree very closely over my entire size range with estimates I obtained using the regression equation given by Mather and Schuck (1960). The largest difference I found, only 1%, occurred at the lower end of my range of curved fork length values of 200 cm.

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DEVELOPMENTAL ANATOMY AND INFLATION OF THE GAS BLADDER IN STRIPED BASS, *MORONE SAXATILIS*

In 1974, a percentage of striped bass, *Morone saxatilis*, fingerlings reared at the Cooperative Fishery Research Laboratory, Southern Illinois University, lacked an inflated gas bladder. The purpose of this study was to describe the developmental anatomy of the gas bladder and its associated structures in striped bass so that a better understanding of the inflation mechanism could be obtained.

With regard to gas bladder morphology, bony fishes are classified as physostomes or physoclists. Generally, the more ancient, soft-rayed fishes (Malacopterygii) are physostomous, while the more modern, spiny-rayed fishes (Acanthopterygii) are physoclistic (Lagler et al. 1962). A physotome possesses a hollow connection, the pneumatic duct, between the gut and the gas bladder throughout its entire life. Some physotomes gulp surface air through the pneumatic duct to initiate inflation of the gas bladder (Tait 1960). Fish that are physoclistic do not possess this open connection as adults. Some physoclists, however, do possess a pneumatic duct as larvae, but the duct atrophies prior to adulthood. Günther's (1880) examinations have shown that adult striped bass are physoclistic. Doroshev and Cornacchia (1979) give a partial description of the development of the gas bladder in striped bass.

Several theories have been advanced to explain how the gas bladder is initially inflated in fishes that do not gulp surface air or are physoclistic prior to initial inflation. Some of these theories include: gases produced by the disintegration of organic materials (Powers 1932); production of gasses as a result of digestion (Johnston 1953); vacuolation of the gas bladder epithelia (McEwen 1940); and functioning of a rete mirabile, or gas gland (Schwarz 1971).

Methods

Histomorphological Studies

Striped bass larvae were obtained from the Hudson River, N.Y., and Lake Charles, La. Upon arrival, the 1- to 4-day-old larvae were transferred into 200 l aquaria and maintained at 16°-18° C. Brine shrimp, *Artemia salina*, were fed regularly to the larvae. Eighty-three striped bass larvae 4.3-24 days old (from the time of hatching) were removed from the aquaria and prepared for histological study. The larvae were fixed in either 10% Formalin[1] or Bouin's fluid, dehydrated in a series of graded alcohols, cleared in benzene, and embedded in Carbowax. From a representative

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

series of 34 larvae, we prepared transverse and longitudinal series sections 7 and 10 μm thick (Table 1). The mounted specimens were stained with either Harris's hematoxylin and eosin or a modification of Mallory's connective tissue stain (Martan[2]).

TABLE 1.—Number of striped bass larvae sectioned to determine the internal anatomy of the gas bladder and its associated structures.

Age (days)	With inflated gas bladder	Without inflated gas bladder
4.3	1	2
4.8	2	3
5.5	2	2
6.0	5	1
7.0	2	0
8.0	2	2
14.0	0	3
21.0	0	1
24.0	4	2

Results

During laboratory aquaria experiments, striped bass larvae were observed with inflated gas bladders as early as day 4. A peak period of inflation occurred during day 5, closely corresponding with the absorption of the yolk sac. Doroshev and Cornacchia (1979) found that striped bass inflated their gas bladder from the 5th to the 7th day.

Striped bass larvae with inflated gas bladders were easily distinguished from larvae with uninflated gas bladders. Morphologically, the newly inflated gas bladder has the general appearance of a small air bubble, located dorsal to the gut. Behaviorly, larvae that had inflated gas bladders oriented horizontally within the water column and maintained their position without continual swimming motion. Larvae without inflated gas bladders assumed a vertical swimming position, sinking when swimming movements ceased. This characteristic swimming behavior of larvae with noninflated gas bladders was defined as "swim-up" behavior.

In 4.8-day-old striped bass larvae, the noninflated gas bladder primordium was dorsal and slightly posterior to the junction of the esophagus and the stomach. The stomach was at the right of the dorsomedial gas bladder primordium. The walls of the noninflated gas bladder primordium were much thicker ventrally than either dorsally or laterally. Columnar epithelium comprised the ventral mass of the gas bladder primordium. The noninflated gas bladder possessed a slight, dorsally located lumen. An open pneumatic duct connected the foregut with the right side of the posterior wall of the gas bladder primordium. The duct was composed of a single layer of cuboidal epithelium, surrounded by a layer of connective tissue.

A network of arterioles and venules, a rudimentary rete mirabile, ran parallel and ventral to the noninflated gas bladder primordium. At the posterior end of the gas bladder, the rete arterioles and venules turned dorsoanteriorally and entered a layer of loose connective tissue adjacent to the ventral columnar epithelium of the gas bladder. Within this connective tissue, a network of capillaries connected the arterioles and venules. Since the rete mirabile proceeded directly to the secretory epithelium of the gas bladder, the whole structure may properly be called a gas gland (Steen 1970). A gas gland is formed in striped bass before the initial inflation of the gas bladder.

In older (8 days) striped bass larvae that still had a noninflated gas bladder, the capillary network was more developed and pushed closer to the ventral columnar epithelium of the gas bladder. This gave the epithelium a festooned appearance.

In striped bass larvae that were in the process of inflating their gas bladders, the initial inflation occurred at the anterior end of the gas bladder. The columnar epithelium, which previously had dominated the ventral wall of the gas bladder, became confined to the posterior portion of the gas bladder as inflation progressed. At no time were distinct vacuoles visible within the ventral, columnar epithelium.

In 5.5-day-old striped bass larvae that possessed an inflated gas bladder, the ventral epithelium was reduced to cuboidal epithelium and was restricted to the posteriorventrad portion of the gas bladder where it was in close association with the gas gland. The remaining walls of the inflated gas bladder were composed of stretched epithelium. The rete mirabile still ran parallel and ventral to the newly inflated gas bladder. Capillaries of the rete mirabile made contact with secretory epithelium towards the posterior of the gas bladder.

In all striped bass larvae which were 4.3-5.5 days old and possessed an inflated gas bladder, a

[2]Martan, J. 1968. Laboratory instructions: Histological techniques in zoology. South. Ill. Univ., Carbondale, 98 p.

pneumatic duct with a well-defined lumen still appeared to form a connection between the gut and the gas bladder. However, in the older larvae of this group, the lumen of the pneumatic duct was smaller. In some sections, the openings between the pneumatic duct and the gut and the pneumatic duct and the gas bladder were not plainly visible, indicating that the pneumatic duct was beginning to atrophy.

We examined 14- and 21-day-old striped bass larvae without inflated gas bladders, and 24-day-old larvae with and without inflated gas bladders. In 14-, 21-, and 24-day-old larvae that had noninflated gas bladders, a well-developed rete mirabile still ran ventral and parallel to the gas bladder, turning dorsally to make a medial connection. The retail capillary network was developed, distending the overlaying connective tissue into a villuslike structure which was bordered by the ventral, columnar (secretory) epithelium of the gas bladder. The villuslike projections occupied most of the internal volume of the gas bladder. The pneumatic duct was well defined and continued to connect the gut with the gas bladder.

In 24-day-old striped bass larvae that had inflated gas bladders the pneumatic duct was absent. Unfortunately, we did not collect any striped bass larvae with inflated gas bladders between day 8 and day 24. We were thus unable to accurately describe the atrophication of the pneumatic duct, which seemingly occurs after inflation of the gas bladder. The rete mirabile was connected to a narrow band of cuboidal epithelium at the ventromedial wall of the gas bladder.

Discussion

Striped bass larvae possess an open pneumatic duct. An experiment designed to determine if striped bass have to gulp surface air to initiate gas bladder inflation was inconclusive, as was a similar experiment conducted by Doroshev and Cornacchia (1979). However, allowing striped bass larvae unobstructed access to the surface did not guarantee inflation in either study.

In our study, the pneumatic duct had atrophied in 24-day-old larvae which had inflated their gas bladders, but an open pneumatic duct was still present in 24-day-old larvae which had not inflated their gas bladders. This suggests that inflation of the gas bladder stimulates the atrophication of the pneumatic tube in striped bass. Johnston (1953) observed a similar phenomenon in the largemouth bass, *Micropterus salmoides*.

The rete mirabile, or gas gland, is developed before initial inflation of the gas bladder in larval striped bass. Since the gas gland concentrates gases within the gas bladders of many adult fishes, it is reasonable to assume that the gas gland plays a role in achieving initial inflation of the gas bladder in larval striped bass. The continued presence of a gas gland, and the prolonged retention of an open pneumatic duct in striped bass larvae that had not achieved initial inflation of the gas bladder within 24 days suggests that initial inflation may occur over an extended period of time.

Other workers have indicated that failure to initiate inflation of the gas bladder may lead to slower growth rates (Tait 1960), a higher percentage of morphological abnormalties (Baker[3]), and an increased susceptibility to stress (Lewis et al.[4]). Studies designed to define the stimuli responsible for the initiation of gas bladder inflation in striped bass, an important sport fish species that is often cultured, would be beneficial.

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[3]Baker, J. F. 1975. The rearing of Hudson River striped bass at the Edenton National Fish Report prepared for Consolidated Edison Company of New York, Inc., 30 p.

[4]Lewis, W. M., R. C. Heidinger, and B. L. Tetzlaff. 1977. Striped bass rearing experiments 1976. Report prepared for Consolidated Edison Company of New York, Inc., 197 p.

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FOOD OF AGE 1 AND 2 ATLANTIC TOMCOD, *MICROGADUS TOMCOD*, FROM HAVERSTRAW BAY, HUDSON RIVER, NEW YORK

Atlantic tomcod, *Microgadus tomcod* (Walbaum), are opportunistic feeders (Howe 1971; Grabe 1978) with amphipods *Gammarus* spp. and the decapod *Crangon septemspinosa* identified as primary prey (Howe 1971; Alexander 1971; Scott and Crossman 1973; Grabe 1978; Nittel[1]). Limited data are available on the biology of yearling and older Hudson River tomcod due to their low overall abundance and because they are most abundant during winter when ice cover restricts sampling. This note summarizes feeding data of 339 tomcod, ages 1 and 2, from the Haverstraw Bay area of the Hudson River (37.5-41.5 mi north of the Battery, New York City) on 19 dates, January 1973-June 1976, and supplements food preference data on juveniles (Grabe 1978). All fish were collected as part of an ecological monitoring program conducted by Lawler, Matusky & Skelly Engineers for Orange and Rockland Utilities, Inc.

Methods

Collections (Table 1) were made with a 9.1 m otter trawl (64 mm mesh cod end liner) towed against the tide at 1.5-2.0 m/s during both day and night. The data are likely to be biased towards daytime feeding preferences since almost twice as many tows were taken during daytime as at night. Diel differences in feeding could not be evaluated because day and night collections were often combined for other analyses. Fish were preserved in 10% buffered Formalin.[2] In the laboratory they were measured (±1 mm total length, TL) and weighed (±0.1 g), and the stomachs were removed and preserved in 70% ethanol. Prey were identified and counted, and the contents of 195 stomachs were dried at 103° C. The number of fish per sampling period whose stomach contents were analyzed were limited by contract and were randomly selected from the total catch. Whenever possible, I analyzed additional fish to increase both sample size and temporal coverage. Yearling and older tomcod collected during fall 1973 were separated from young-of-the-year by examination of length-frequency histograms drawn from larger samples (Lawler, Matusky & Skelly Engineers[3]); by this method age 1 and 2 fish were those ≥160 mm TL. On other sampling dates young-of-the-year were present only as larvae or as juveniles <110 mm TL.

TABLE 1.—Collections of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

Season	Sample size	Total length (mm) Mean	95% confidence limits
Winter (Jan.-Feb.)	72	130.5	126.2-134.7
Spring (Apr.-June)	166	158.7	155.8-161.6
Summer (July-Aug.)	10	156.3	142.2-170.3
Fall (Oct.-Dec.)	91	182.6	178.3-186.8

Food preference data were classified seasonally and examined as percentage occurrence (number of fish in which prey item "a" occurred/total number of fish), percentage composition (number of prey item "a"/total number of prey), and as importance, I, the geometric mean of these two measurements (Windell 1971). This approach, however, may overestimate the utilization of smaller prey (e.g., copepods) but should provide a better indication of feeding preference than either percent occurrence or percent composition taken singly. An index of fullness (Windell 1971), I_f, was calculated to evaluate feeding intensity (dry

[1]Nittel, M. 1976. Food habits of Atlantic tomcod (*Microgadus tomcod*) in the Hudson River. *In* Hudson River Ecology. Fourth Symposium on Hudson River Ecology. Bear Mountain, N.Y., March 28-30 1976. Hudson River Environmental Society, Inc.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Lawler, Matusky & Skelly Engineers. 1976. Environmental impact assessment—water quality analysis: Hudson River. Natl. Comm. on Water Quality. NTIS PB-251099.

weight of stomach contents × 10^4 as a percentage of wet weight of fish). Empty stomachs were included in seasonal measurements of feeding intensity. Statistical tests were from Sokal and Rohlf (1969).

Results and Discussion

Gammarus spp. were the most important prey during all seasons (Table 2). Secondary prey included copepods (winter), the oppossum shrimp, *Neomysis americana* (spring and fall) *Monoculodes* sp. (Amphipoda) (spring), *Cyathura polita* (Isopoda) (spring and fall), and sand shrimp, *Crangon septemspinosa* (fall). *Gammarus* spp., *N. americana,* and *Monoculodes* sp. are numerically important tychoplankters in this area of the Hudson River (Ginn 1977; Lauer et al.[4]). Abundant infaunal species in the Haverstraw Bay area include the polychaete *Scolecolepides viridis* the amphipod *Leptocheirus plumulosus,* and *Cyathura polita* (Ristich et al. 1977). Tychoplankton appears to be more important as prey of Hudson River tomcod than infauna. In other estuaries, however, infauna may be more important; e.g., Alexander (1971) found that polychaetes, even though

[4]Lauer, G. J., W. T. Waller, D. W. Bath, W. Meeks, R. Heffner, T. Ginn, L. Zubarik, P. Bibko, and P. C. Storm. 1974. Entrainment studies on Hudson River organisms. *In* L. D. Jensen (editor), Entrainment and intake screening. Proceedings on the second entrainment and intake screening workshop, p. 37-82. Johns Hopkins Univ. Edison Electric Inst. Rep. 15.

TABLE 2.—Seasonal prey of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

Taxon	Percent occurrence[1]				Percent composition[2]				Importance[3]			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Nematoda		0.6		2.2		<0.1		0.1		0.1		0.5
Polychaeta:												
Scolecolepides viridis		2.4		2.2		0.1		0.1		0.5		0.5
Oligochaeta				1.1				0.4				0.7
Hirudinea		1.2		2.2		0.1		0.2		0.3		0.7
Glossiphoniidae	6.9			0.3					1.4			
Helobdella sp.		0.6				<0.1				0.1		
Theromyzon sp.		2.4				0.2				0.7		
Piscicola milneri		0.6				<0.1				0.1		
Mollusca:												
Amnicola sp.		1.2		1.1		<0.1		0.1		0.2		0.3
Crustacea:												
Ostracoda		0.6				<0.1				0.1		
Copepoda	45.8	4.8		2.2	47.7	1.3		0.3	46.7	2.5		0.8
Mysidacea:												
Neomysis americana	13.9	18.1	10.0	40.7	2.9	3.5	12.5	9.6	6.3	8.0	11.2	19.8
Isopoda:												
Chiridotea almyra		6.6				0.3				1.4		
Cyathura polita	2.8	18.7		14.3	0.1	0.9		2.3	0.5	4.1		5.7
Edotea triloba	1.4			5.5	0.1			0.5	0.4			1.7
Amphipoda:												
Corophium lacustre	1.4	1.8		2.2	0.1	0.1		0.1	0.4	0.4		0.5
Gammarus spp.	81.9	87.3	60.0	64.8	43.5	88.6	62.5	70.2	59.7	87.9	61.2	67.4
Leptocheirus plumulosus		6.6		1.1		0.3		0.1		1.4		0.3
Melita nitida				1.1				0.1				0.3
Monoculodes sp.	12.5	13.3		14.3	2.0	4.0		3.0	5.0	7.3		6.5
Decapoda:												
Callinectes sapidus				5.5				0.6				1.8
Crangon septemspinosa	1.4		30.0	49.1	0.1		18.8	7.2	0.4		23.7	18.8
Rhithropanopeus harrisii		1.2		20.9		0.1		2.3		0.3		5.7
Insecta:												
Odonata:												
Enallagma spp.		0.6				<0.1				0.1		
Trichoptera larvae		0.6		1.1		<0.1		0.1		0.1		0.3
Diptera:												
Chaoborus punctipennis larvae		1.8	10.0	1.1		0.1	6.2	0.1		0.4	7.9	0.3
Chironomidae larvae	2.8	4.8		4.4	0.1	0.2		0.7	0.5	1.0		1.8
Unidentified pupae		1.8				0.1				0.4		
Pisces:												
Alosa spp.				5.5				0.6				1.8
A. aestivalis				*								
A. pseudoharengus				*								
Anchoa mitchilli				2.2				0.1				0.5
Anguilla rostrata		0.6				<0.1				0.1		
Microgadus tomcod eggs	4.2				3.3				3.7			
M. tomcod larvae		1.2				0.1				0.3		
M. tomcod juveniles		1.8				0.1				0.4		
Unidentified	1.4	3.6		14.3	0.1	0.1		1.1	0.4	0.6		4.0

[1]Number of occurrences/total number of fish.
[2]Number of prey item "a"/total number of prey.
[3]Geometric mean of (percent occurrence × percent composition).

underestimated, ranked second to *Crangon septemspinosa* in the percent volume of stomach contents of tomcod from Montsweag Bay, Maine.

Feeding intensity showed significant differences between seasons by analysis of variance using arc-sine transformed I_f values ($F_{3,190} = 11.9$; $P<0.001$). A Student Newman-Keulls test showed that I_f was greatest during fall, and spring values were greater than winter and summer, which were similar ($P<0.05$) (Table 3). Percentage of empty stomachs was highest during winter, least during fall and spring. Feeding intensity, then, was greatest both prior to and subsequent to spawning, when, presumably, energy requirements were greatest. A similar seasonal cycle was described for juveniles (Grabe 1978).

A shift in importance of primary prey, from *C. septemspinosa* to copepods, occurred from fall to winter. A similar shift from the larger prey to smaller prey was noted for juveniles (Grabe 1978), and it was suggested that constriction of the alimentary canal by maturing gonads (Schaner and Sherman 1960) was a factor. To clarify this shift, predation on the primary species (*Gammarus* spp.) and large (*C. septemspinosa*) and small (copepods) secondary prey were examined for the period November 1974 through February 1975 (November and December fish were young-of-the-year; data summarized in Grabe 1978). *Gammarus* spp. were important throughout this period, especially on 4 December (Table 4). *Crangon septemspinosa* was important only during November and copepods were important during January and February. Since gonad production was generally greatest November through December and coefficient of maturity peaks during November for males and January for females (Orange and Rockland Utilities, Inc.[5]), the observed shift in prey selection corresponded well with gonad maturation. Causation has yet to be determined and small sample sizes may not depict the situation accurately.

Tomcod are occasionally piscivorous (Alexander 1971; Scott and Crossman 1973; Nittel see footnote 1). Five fish species, including eggs, larvae, and juvenile tomcod were identified as prey and were most important during the fall (Table 2). Cannibalism occurred at low levels during winter and spring. Cannibalism has been reported in other fishes, e.g., *Alosa pseudoharengus* (Rhodes et al. 1974) and *Stizostedion v. vitreum* (Chevalier 1973) and may be a factor affecting recruitment.

TABLE 3.—Index of fullness[1] (for subsamples) and percentage of empty stomachs of age 1 and 2 Atlantic tomcod from Haverstraw Bay, Hudson River, 1973-76.

Season	Sample size	Index of fullness: Mean	Index of fullness: 95% confidence limits	Percent empty[2]
Winter	70	6.21	4.19- 8.23	12.5
Spring	68	10.24	7.94-12.53	4.2
Summer	5	0.32	0.09- 0.55	10.0
Fall	52	20.62	12.08-29.12	3.3

[1]Dry weight of stomach contents × 10^4 as a percentage of wet weight of fish.
[2]Based on total number of fish analyzed; see Table 1.

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[5]Orange and Rockland Utilities, Inc. 1977. Bowline Point Generating Station: Near-field effects of once-through cooling system operation on Hudson River biota.

TABLE 4.—Changes in the importance of *Crangon septemspinosa* (CS), copepods (Cop), and *Gammarus* spp. (Gamm) in the diet of Atlantic tomcod from Haverstraw Bay, Hudson River during the period November 1974 through February 1975.

Date	Sample size	Percent occurrence[1]			Percent composition[2]			Importance[3]			Mean number/stomach		
		CS	Cop	Gamm	CS	Cop	Gamm	CS	Cop	Gamm	CS	Cop	Gamm
5 Nov.	14	57.1	0.0	85.7	14.8	0.0	77.4	29.1	0.0	81.4	1.2	0.0	6.4
13 Nov.	13	69.2	0.0	46.2	41.2	0.0	23.5	53.4	0.0	33.0	2.2	0.0	1.2
4 Dec.	28	0.0	7.1	100.0	0.0	0.2	95.4	0.0	1.2	97.7	0.0	0.1	48.9
25 Jan.	15	6.7	73.3	66.7	0.1	68.1	18.7	0.9	70.7	35.3	0.1	39.1	10.7
19 Feb.	4	0.0	75.0	75.0	0.0	26.3	61.1	0.0	44.4	6.7	0.0	11.5	26.8

[1]Number of occurrences/total number of fish.
[2]Number of prey item "a"/total number of prey.
[3]Geometric mean of (percent occurrence × percent composition).

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1) Page 713, right column, line 13, correct line to read:
Data from haul 8 are biased toward larger indi-

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